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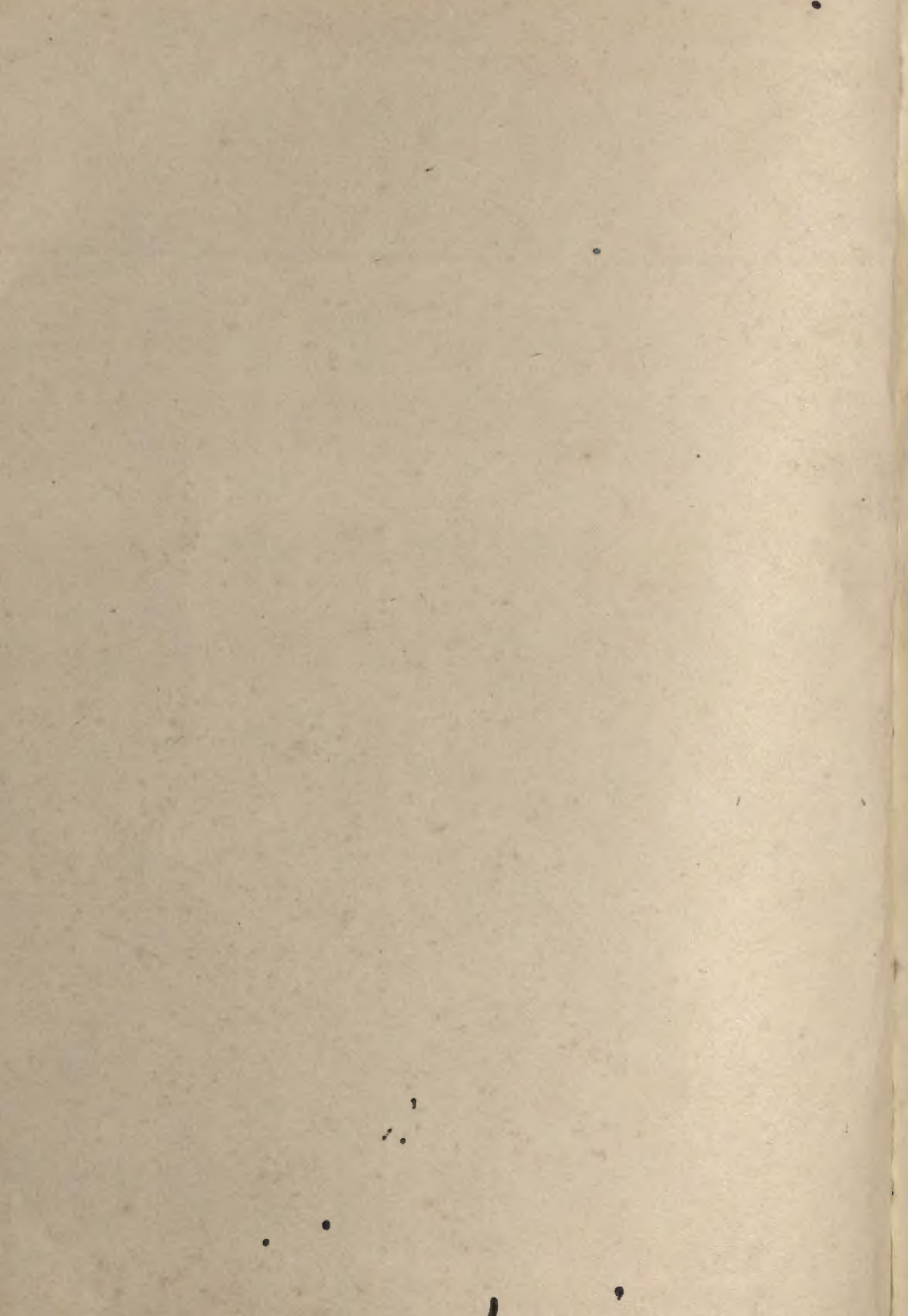
N. Buffaloe & J. Throneberry

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Principles
of
biology



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biology

2nd edition

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by Neal Buffaloe and J. B. Throneberry

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*To
Inez
and
Barbara*

Preface

The first edition of this book was written primarily for the one-semester course in elementary biology, and the project was originally undertaken by the senior author because he wished to develop a viewpoint for the brief course. The philosophy behind this viewpoint is expressed by the following excerpts from the preface to the first edition:

... the exhaustive text fails to satisfy every teacher of biology, especially for use in certain types of introductory courses. For example, many colleges offer a one-semester course in connection with a program of general education, and teachers often experience difficulty in adapting such a course to a book so packed with information that there must of necessity be a great deal of picking and choosing. The student frequently feels overwhelmed by sheer weight, and the greatest strength of many a fine and lengthy text, its thoroughness, becomes its greatest weakness in a brief course. . . .

This book constitutes a mild revolt against what appears to be an almost frantic race for volume and abundant description. It is believed that it will serve best as a nucleus around which the resourceful teacher may synthesize the cytoplasm of a successful course, . . . the author is of the conviction that a principles approach, aimed at fundamental life processes and related to other fields than biology, is far more valuable to the college freshman than is a course which is largely devoted to the memorization of descriptive and perhaps isolated information.

In the main, we have attempted to retain the overall approach of the first edition with some addition of depth and a greater degree of continuity. There is a completely new emphasis upon levels of organization and the appearance of emergent properties at successively higher levels. We have also attempted to relate energy transformations to the structure and function of living systems at different levels of organization. Although all former chapters have been modified to some extent, Chapters 2, 3, and 6 have been completely rewritten. A new chapter on regulation and control (Chapter 5) now precedes chapters dealing with metabolism, growth, reproduction, responsiveness, and adaptation, respectively. Our main discussion of evolution remains near the end of the book for what we believe are good reasons, but sufficient material has been added to give it a chapter heading of its own.

Although it would be impossible to acknowledge all the help we have received, we wish especially to thank Professors A. J. Bernatowicz, Thomas J. Burgess, Richard A. Collins, Harold E. Cooper, Ray Kinser, Robert T. Kirkwood, J. M. Manion, Jewel E. Moore, and James H. Ware. We are extremely grateful to the many teachers and students who took the time to offer criticisms, and we hope they will not hesitate to do so again. It would be difficult to imagine working with a more cooperative and helpful staff than that of Prentice-Hall; their assistance has gone far beyond a mere contractual obligation.

We hope and trust that this book will prove to be a contribution to the teaching of biology.

Neal D. Buffaloe
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Conway, Arkansas

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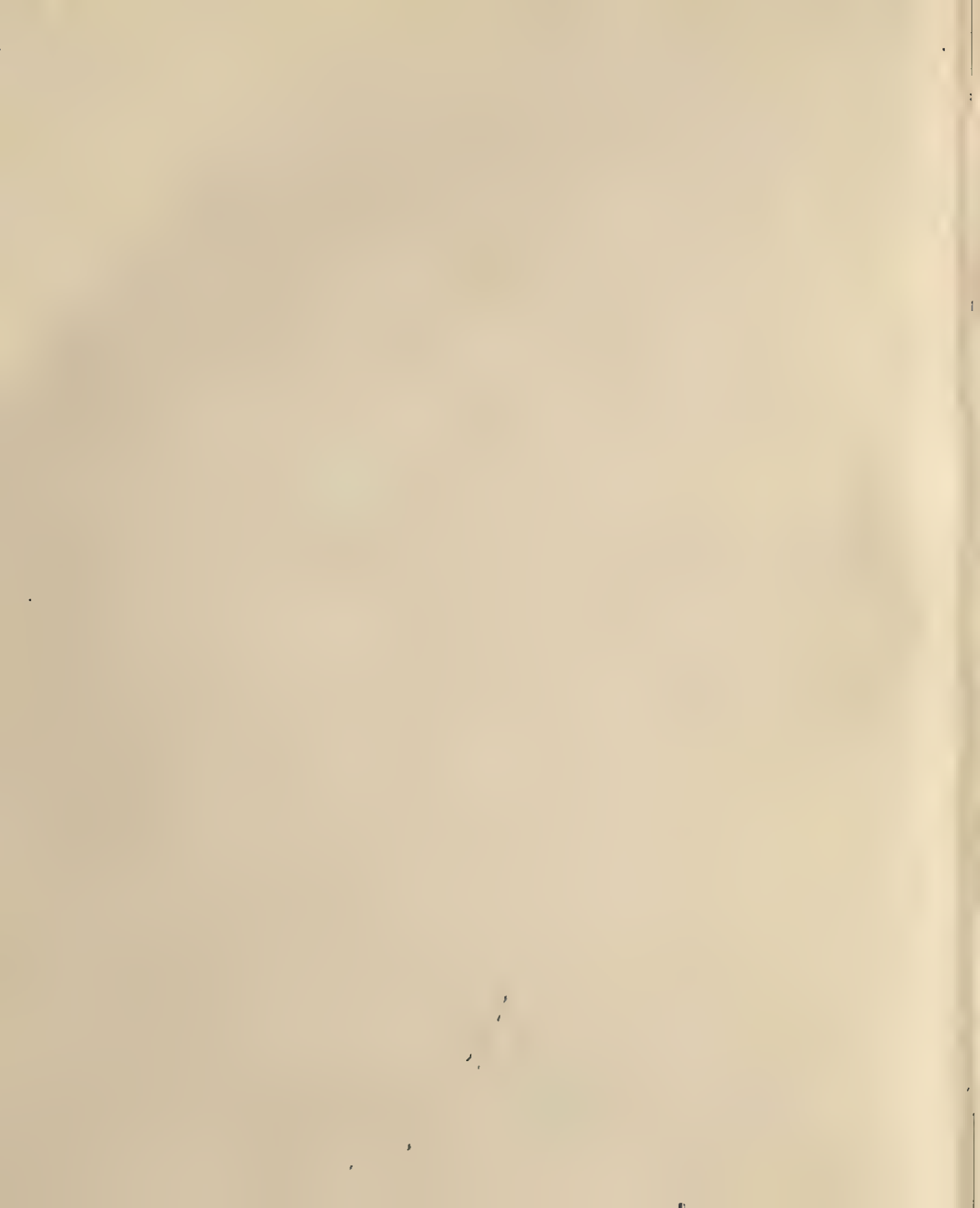
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Principles
of
biology



1

Science and biology

The human mind is a marvelous entity. Among other things, it enables us to associate ideas and insights with words or phrases. In a sense, then, a word is shorthand for a concept which takes the form of a thought pattern.

There is no guarantee, of course, that the pattern will be complete or even correct, and it is inevitable that any given person will react to a word differently from the way another person might react. This is particularly true of a word which describes a concept of great scope or a broad field of activity. The term "biology," for example, produces a variety of thought patterns in the minds of a variety of people, depending on their background experience. A person who has taken a course in biology, perhaps as a high-school student, may associate numerous scholastic experiences with the word. Still another person, with less formal but perhaps more direct experience with the world of life, may call to mind a greenhouse, a herd of deer, an alpine meadow, or an impressive display of prehistoric animals.

On the assumption that your concept of the term biology needs to be enlarged, regardless of your background experience, the college of your choice offers a course in introductory biology. This is the text your teacher has chosen to follow. You may be familiar with the material represented, in which case it should be possible for you to acquire greater depth and meaning with regard to such material. Other concepts will be new to you. In any event, it becomes a challenge to your teacher to present the principles of biology in such a way that you leave the course with a far more intelligent and meaningful idea of this area of human interest than you previously had entertained. As a result, in the course of your studies, you may experience a change in attitude from indifference or disdain to respect and, finally, to a full appreciation for and interest in a field that is one of the more dynamic intellectual disciplines.

- 1.1 On the nature of science By way of introduction to the field of biology, it seems logical to direct some attention toward its relation to other sciences. Although the word from which "science" is derived (L. *scientia*, knowledge) was once used in regard to knowledge of any sort, present-day meaning restricts it to knowledge which depends upon insights gained through observation and experimentation, as contrasted to that which comes to us through tradition or sheer reason. Whereas most of the so-called *social sciences* rely primarily upon tradition and sheer reason as knowledge sources, the *natural sciences* (those dealing with phenomena of our material universe) rely primarily upon observation and experimentation; yet the distinction between these two areas of science is somewhat nebulous. For example, a behavioristic psychologist might well fit our definition of a natural scientist better than some biologists who, in popular usage, are classified

as natural scientists. Nevertheless, the word *science* most commonly means natural science.

Traditionally, the natural sciences have been divided into two categories: The *physical sciences*, such as physics, chemistry, and geology, have been defined as those natural sciences which deal with "nonliving" phenomena. Those natural sciences which deal with "living" phenomena have all been included in one large area, *biology* (Gr. *bios*, life + *logos*, discourse), which is the science of organisms. Although this is a convenient and operationally useful distinction, it is clearly not logical, as will become apparent in our further discussion. For example, as we shall see, living systems must frequently be approached by means of physical and chemical concepts.

Perhaps it is in order at this point to attempt a further clarification of what we mean by the term science, and how it differs as an activity from other endeavors on the part of man. Actually, this is a difficult task, because there are many ways of looking at science and, indeed, of engaging in it as an activity. We shall only attempt to suggest a few guidelines, and if these arouse sufficient interest in the subject, the references at the end of this chapter will provide a means for pursuing the subject further.

Let us begin by mentioning three basic assumptions which scientists take for granted:

1. *Science deals with observable phenomena in a material universe.* By "observable," we mean that they can be apprehended, measured, or approached by means of human senses or by instruments capable of translating objective data to the human mind. This is not to suggest that science denies the existence of other types of realities, for example, nonmaterial or supernatural phenomena. We are only saying that science, in its accumulation of data, is limited to things that have a material existence. For example, science cannot approach these questions: Is there a God? Does the universe exist for a purpose? Are there absolute moral values for man? If these are meaningful questions, and they are, they lie outside the realm of science. The scientist, as a *scientist*, must *act as if* they have no meaning for him. This sometimes leads to confusion in understanding science, because some people take this "act as if" self-discipline on the part of the scientist quite literally. Actually, there are many legitimate areas of human thought where science is powerless, and it is best that we identify these limitations and recognize them for what they are.

2. *Science assumes a uniformity in the material universe*, that is, phenomena are reproducible because the fundamental characteristics of the universe as we know it are constant. For example, if

objects of varying weights dropped from the leaning tower of Pisa reached the ground at approximately the same time over 300 years ago, we can expect them to do so today. The uniformity principle does not suggest that nature is rigid and that no changes occur. It is simply the assumption that effects have causes, and that we have to take this for granted in performing scientific work. An opposing concept to science in this respect is magic—not a very fruitful assumption in any area of human endeavor.

3. *Science does not deal with certainties, but with probabilities.* At first inspection, this seems to contradict our second assumption. However, we must understand that *uniformity* and *rigidity* are two entirely different things. For example, we may observe that clover leaves consist of three leaflets, and this may be verified by a hundred successive observations. But it is patently impossible to examine all the clover leaves in the world, so that we cannot state *with certainty* that all clover leaves have three leaflets. The probability is extremely high, though, that any given clover leaf will conform to the general rule. This is consistent with the uniformity principle, and it also verifies our assumption in regard to certainty versus probability.

There are other assumptions governing science and scientific endeavor, but they are by and large extensions of these three. It should be understood that science operates at different levels of sophistication. In the course of his work, a scientist may take for granted various assumptions that may be peculiarly applicable to his problem. He may not even consciously keep these in mind while he is working—rather, they (and the three assumptions listed above) become intuitive thought processes which govern his work.

For the moment, let us devote further attention to our third basic assumption, not that it is more important than the other two, but because it is more essential to a clarification of certain common misunderstandings of the nature of science. First of all, let us consider an example.

Suppose a person owns a plot of ground which consistently yields a poor corn crop. He focuses his attention on this problem and begins to search for possible reasons why this should be so. His train of thought might run something like this: "Perhaps there is not sufficient rainfall on this ground. No, this could not be the answer because another plot just across the road from mine consistently yields a good crop. Perhaps it is not cultivated as thoroughly as it should be. This could be the cause, although I believe that it is plowed as much as the plot across the road. Maybe there is a deficiency of nitrogen in the soil. At least, this would be a starting point."

Notice that our investigator has considered three possibilities regarding the problem. He has rejected one completely, and of the

other two, one seems more likely than the other. Thus, he has selected a tentative explanation, which may be called a *hypothesis* and which is of value at this point only as a means of approaching the problem. His next step is clear. In order to test his hypothesis, he must administer nitrogen to the soil. He may encounter additional problems at this point in regard to the quantity of nitrogen needed, but in time he will either strengthen or invalidate his hypothesis. If he invalidates it, he will be obliged to formulate a new hypothesis and start over. However, let us suppose that he adds nitrogen and does produce a better crop. Is he justified in considering the problem solved? Actually, he has only strengthened his hypothesis. However, if he continues to produce good crops by the addition of nitrogen, his hypothesis becomes more than just a suspicion. *It has gained predictive value* because he knows now what to expect when he administers nitrogen. This is true because he has verified the strength of his hypothesis through repetition of the experiment. At this point, the generalization may be called a *theory*.

Perhaps most people would be content to let the problem rest here because, for all practical purposes, it seems to be solved. As a matter of fact, all that has been shown thus far is that the addition of nitrogen has probably increased crop yield in this one particular instance. It cannot be stated with certainty that there was a nitrogen deficiency, and it is at this point that the importance of *control* experiments is made clear. By a control, the scientist means an experiment to compare what would have happened had the variable factor (in this case, addition of nitrogen) *not* been put into the main experiment. In order that the hypothesis of nitrogen deficiency may be subjected to a critical test, therefore, the investigator should reserve a part of his field for *no nitrogen treatment*. Then (assuming that all other variables are ruled out) a difference in yield between the experimental and control plots is sufficient ground for saying that there was a nitrogen deficiency in this particular field. In other words, the degree of probability has been greatly increased.

Let us note carefully that the investigator is able to broaden his theory at this point. His former one, limited in use to his own field of corn, may now be enlarged to include other fields as well. It might be stated something like this: "When the yield of a corn crop is below expectation, and other common factors associated with crop failure have been ruled out, the addition of nitrogen will increase yield." Perhaps he is not interested in following through on this theory, but if he does, it is certain that it will, in turn, give rise to other theories. *This is one of the basic features of scientific procedure, namely, that one theory leads to other theories, which sometimes replace it or*

render it obsolete. This, then, is the major activity of science—the formulation and use of theories.

Let us return to our assumption that science does not deal with certainties, but with probabilities. Most people think that the major activity of science is the discovery of facts, or certainties. *Strictly speaking, there is no such thing as a scientific "fact" or "truth."* Fact and truth are terms which are meaningful only in a historical or possibly a philosophical sense.* To illustrate, suppose a person makes this statement: "I spent last evening with my grandmother, who lives in Thornburg." If this is true, it is only true historically. No amount of experimentation or present observation can decide the issue one way or the other. Now consider this statement: "If a person swallows a gram of potassium cyanide, it will kill him." Probably, this is as "true" as scientific statement can become, but it cannot be called a fact until it is historically proven. Even then, it would be true of only one person at a time! This distinction may seem tedious, but it is the only framework within which the scientist can operate. It is for this reason that he speaks of *data* rather than *facts* and that he uses the term *theory* to replace the word *truth*.

The role of theory in science is subject to widespread misunderstanding. To most people, this term suggests some sort of wild guess. "I have a theory that Johnny inherited his distaste for onions from his Uncle Jack," might observe a fond mother. We will not pause to dwell on the possibilities for scientific criticism in such a statement, except to note that the observation has absolutely no predictive value. Inasmuch as it does not lend itself very readily to any sort of testing (at least by a person who is unfamiliar with behavioral science), the statement hardly ranks as a hypothesis. To look at another aspect of the problem, a scientist may advance a theory, and call it such, which is given some attention by the popular press. It is immediately discounted by numerous people, especially if it intrudes upon their prejudices in any way. "We want facts, not theories," is a frequent reaction.

Unfortunately for those who seek simple answers to complex problems, science is only incidentally concerned with facts. About the best that can be done to make a theory a fact is to call it a *principle* when it is so universally reliable in predictability as to be almost absolutely dependable. This is especially true if it has a broad application in scientific work. It may even be called a *law* in such cases, although there is a growing conviction among scientists that this

* Of course, we sometimes use these terms in a purely literary sense, as in the expressions "It is true that . . .," "As a matter of fact . . .," and so on.

term should be restricted to legal usage.* Presently, we shall introduce an example of a scientific principle.

What, then, is science? One of the great scientists and educators of our century, James Bryant Conant, has defined it as "an interconnected series of concepts and conceptual schemes that have developed as a result of experimentation and observation and are fruitful of further experimentation and observations."† Although this definition is merely one way of looking at science, it is quite workable, and it serves to eliminate many activities which are often termed scientific. Witness, for example, the application of the words *science* and *scientific* to commercial products whose sponsors hope to catch the public imagination with a magic word but whose endeavors are fruitful of no further experimentation and observations except in the realm of advertising! Actually, there is nothing mysterious or even necessarily difficult about the activities to which we refer as science. Although the more complex problems of science require prepared minds for their successful pursuit, almost any person could follow the observational and experimental procedures which were outlined above in regard to the hypothetical corn crop. As applied to natural phenomena, therefore, scientific procedure differs little from "common sense" thinking, except that it becomes more exact and critical in its observations, in its experiments, in its controls, and in its deductions.

Actually, the scientist seldom stops to quibble over the exact distinctions between theories, principles, and laws, and he may use these words rather interchangeably. It is commonly understood, nevertheless, that a principle is something of a "graduated" theory and that a law is still more definite or useful in its application. In actual practice, the working scientist is usually caught up in a maze of difficult questions which involve hypothesis, theory, principle, observation, and experimentation all at one time, to say nothing of basic assumptions and the intuitions he has gained through experience. Even imagination and fortunate accident play an extremely important role in scientific work. An almost unlimited number of examples might be cited to show how these several factors work together. Since time gives us certain advantages of analysis, we shall cite an example from the past century.

Virtually everyone today, whether he is familiar with biology or not, accepts the principle of *biogenesis*, which holds that life comes from life. In other words, it is commonly understood that new organ-

* For an extended discussion of scientific terminology, and especially a criticism of the use of the term law in science, the student is advised to see Kemeny, *A Philosopher Looks at Science* (reference at end of chapter).

† *Science and Common Sense* (New Haven: Yale University Press, 1951).

isms, whether relatively simple or quite complex, spring from parents. It may be surprising to many that as late as the middle of the nineteenth century a controversy was raging among biologists as to whether some living forms arise directly from nonliving matter. It had been successfully shown before this time that animals and plants large enough to be seen with the eye did indeed arise only from parents as far as could be determined, but on the microscopic level, the issue was far from settled. As a generalization, therefore, biogenesis was little more than a hypothesis which was held by one school of biologists.

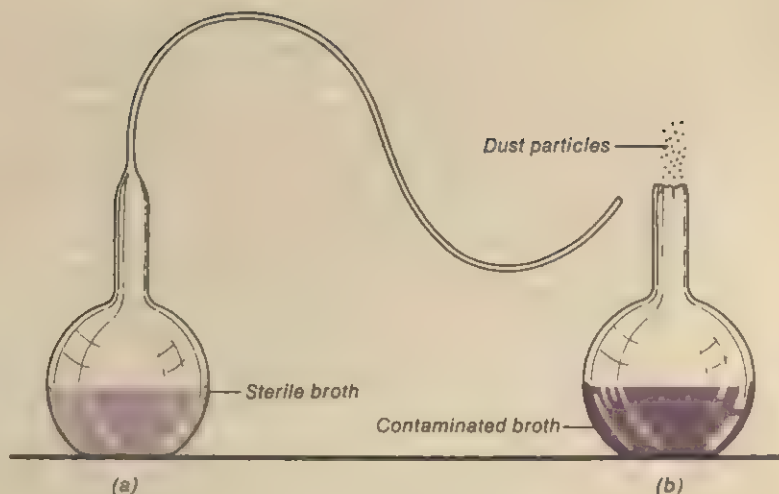
One of the foremost proponents of the theory of biogenesis was a French biologist, Louis Pasteur (1822–1895), who sought to verify it beyond reasonable question. Those who opposed this view held that life developed whenever oxygen came into contact with suitable nutrient materials, and they sought to demonstrate this by heating such materials in order to kill organisms already present (which, as it turned out, they failed to do) and then allowing oxygen to reach them. By about the year 1860, Pasteur had already satisfied himself by experimentation that nutrient materials, upon coming in contact with air, would indeed show within hours the presence of teeming millions of microscopic organisms. His hypothesis was that a number of these were present in the material to begin with, and that heating was not carried on sufficiently long to kill all of them. When enough heat was employed to kill all microorganisms present, he reasoned, the nutrient material should remain free of them unless some were introduced (possibly being carried on dust particles of the air) and allowed to grow.

In order to test this hypothesis, Pasteur devised a most ingenious and simple experiment, which he described as follows (see also Figure 1.1):

I place into a glass flask one of the following liquids, all extremely alterable upon contact with ordinary air, water of brewer's yeast, water of brewer's yeast with sugar added, urine, sugar beet juice, pepper water; I then draw out the neck of the flask in such a way as to give it various curvatures. I then bring the liquid to a boil for several minutes until steam issues freely through the open narrow end of the neck, without any other precautions. I then allow the flask to cool. It is a remarkable thing, likely to astonish everybody used to the delicacy of experiments relating to so-called "spontaneous" generation, that the liquid in such a flask will remain indefinitely unchanged. It may be handled without fear, it may be transported from one place to another, it may be submitted to all the temperature variations of the seasons, and the liquid does not undergo the least alteration. . . .

(It would seem that the ordinary air, entering with force during the first moments, ought to enter the flask in an entirely crude state. This is

Figure 1.1 (a) The type of flask used by Pasteur in his studies on spontaneous generation. Because of the curvature of the neck, dust particles could not enter the flask, but air could. (b) Appearance of flask 24 hours after the neck had been broken. Deeper color of broth represents bacterial growth.



true, but it meets a liquid still at a temperature approaching the boiling point. The entrance of air then occurs more slowly, and when the liquid is sufficiently cooled so as not to rob the germs of their vitality, the entrance of the air is sufficiently slow so that it leaves in the humid curves of the neck all the dust capable of acting on the infusions and there bringing about organized formations. At least, I do not see any other possible explanation for these curious results. For, if after one or several months in the incubator, the neck of the flask is removed by a stroke of the file, without otherwise touching the flask, after 24, 36, or 48 hours, the molds and the infusoria will begin to show themselves exactly as in the open, or as if the flask had been inoculated with dust from the air.*

Although this experiment appears to be quite simple at first inspection, it is really an involved one from the standpoint of scientific procedure. In performing it, Pasteur was obliged to depend upon many theories and principles which had been set forth either by himself in previous experiments or by investigators who preceded him. Notice that in the first sentence he declares that the liquids he uses are "all extremely alterable upon contact with ordinary air." This generalization takes into consideration his previous work with such liquids, the role of oxygen in biochemical activities, and (although not specifically stated) the role of microorganisms in such alterations as he has in mind. In performing the experiment, he utilizes previous knowledge regarding the effect of heat upon experimental materials and upon microorganisms. Even his technical

* From *Annales de Chimie et Physique*, Vol. 64, 1862. Selected from the abridged translation by M. L. Gabriel, which appears in *Great Experiments in Biology* (see reference at end of chapter).

manipulation of the glass necks of his flasks depends upon a physical principle. Almost every sentence of his account (and the entire report is much longer than this excerpt) implies the utilization of previously developed theories and principles. Finally, his own conclusion from the experiment is declared to be a new principle, namely, that life comes only from life, even on the microscopic level.

In order to demonstrate that theories and principles are open to further examination when new evidence appears and that "certainty" is too absolute a term to be useful in science, let us shift the scene to the present day. Although the biogenetic principle still serves as a working basis for biologists, we no longer feel as certain as we once did that it is universally applicable, or at least that it has always been absolutely maintained. For reasons that will be set forth in a later chapter, we believe that we have a workable explanation for the origin of life on this planet (and after all, life had to originate at some point for biogenesis ever to begin). Once we have admitted the necessity for the spontaneous generation of life one time, we cannot logically deny the possibility of its occurrence many times. However, our past experience with organisms indicates that we get along better if we stay within the framework of the biogenetic principle. In other words, *a good theory (or principle, if you please) is one which accounts for more data and is more reliable in predictability than any available alternate theory.* It is *not* one that is the last word in its pronouncements. Science can only pursue truth—it cannot state it.

Thus it is that theories and principles give way to others, forming what Conant calls an interconnected series of concepts and conceptual schemes. In this way, science goes on seeking but, in a sense, never finding. It is content to build scaffolding upon which to stand while it builds a new level on its edifice, then letting the new level itself serve as the scaffolding for a still higher one. Sometimes it has to tear down a portion of what it has built and start over according to newer specifications. Also, it must be content to realize that its building will never be finished, for this is the very essence of science.

1.2 Fields of biology Biology is an exceedingly broad and diverse science. This is a reflection of the many approaches that may be taken to the study of organisms. In order that we may understand something of the several existing viewpoints, let us name and classify some of the more important fields, all of which may be subsumed under the term "biology."

First of all, let us look at fields of biology from a viewpoint of organizational levels. The study of molecules and compounds associated with life is termed *biochemistry*; the study of energetic rela-

tionships in living systems is termed *biophysics*. At a somewhat higher level of organization, the study of cells (the fundamental units of living matter) is called *cytology* (Gr. *cytos*, cell). At a still higher level, the study of tissues (groups of similar cells) is called *histology* (Gr. *histos*, tissue). At the level at which we focus attention upon organisms themselves, we encounter a multitude of fields. Some of the more important ones are *embryology* (Gr. *embryon*, to swell), the study of development; *anatomy* (Gr. *anatomia*, to cut up), the study of structure as determined by dissection; and *paleontology* (Gr. *palaios*, ancient), the study of fossils. Finally, at a still higher level of organization, the study of groups or populations of organisms as they relate to one another and to their environments is called *ecology* (Gr. *oikos*, house). Also at the population level, *taxonomy* (Gr. *taxon*, arrangement) is the study of classification.

Let us return for a moment to the organismic level of organization in the scheme we have just reviewed. From the approach of natural history, we may list several fields which are defined according to the appearance of organisms in nature. It is generally recognized that two great groups of living things exist; with a few exceptions, every organism is considered to be either a *plant* or an *animal*. The study of plants, from whatever standpoint, is called *botany* (Gr. *botane*, plant), and the study of animals is called *zoology* (Gr. *zoon*, animal + *logos*, discourse). Within these two subdivisions of biology, there are still smaller fields devoted to the study of particular groups of plants or animals. Thus the study of mosses is called *bryology* (Gr. *bryon*, moss), the study of fungi is *mycology* (Gr. *mycos*, mold), the study of bacteria is *bacteriology*; that of fishes, *ichthyology* (Gr. *ichthys*, fish), that of reptiles, *herpetology* (Gr. *herpein*, to creep); and so on.

From yet another viewpoint, two broad fields of biology represent different approaches to the study of living systems. These two fields are *morphology* (Gr. *morphos*, form), which is concerned with *structure*, and *physiology* (Gr. *physis*, function), which is concerned with *function*. To illustrate, anatomy is morphological in its orientation. Thus, one may study human anatomy, plant anatomy, the anatomy of birds, and so on, and the viewpoint is morphological throughout. In contrast if one studied the function of the human body, of plants, or of birds, he would speak of human physiology, plant physiology, or avian (L. *avis*, bird) physiology. Other fields, such as embryology or cytology, may be oriented either morphologically, physiologically, or both.

Finally, there are two fields which pervade every viewpoint in modern biology so thoroughly that they must be considered special cases. They are *genetics* (Gr. *genesis*, to be born), the study of heredity, and *evolution* (L. *evolutio*, an unrolling), the study of changes

which have occurred in the world of life over time. The relationship of genetics and evolution to other viewpoints and fields of biology might be illustrated as follows. Let us imagine that we could construct a group of hollow spheres in such a way that the space within one sphere might join and overlap that within another sphere (or spheres). Situated in a three-dimensional continuum, each sphere might be considered to represent a field of biology, and each spatial plane would represent a viewpoint. Now let us connect these spheres with a pair of cords entwined about one another so that they pass through every sphere and connect every one directly to each of the others. This double cord represents genetics and evolution. Probably you will not be able to appreciate this proposed relationship of genetics and evolution to other biological viewpoints or fields at this point, but you might do well to keep it in mind as we proceed through the following chapters.

Now it should not be supposed that a biologist selects some field of interest and then proceeds to isolate himself from the knowledge and techniques of other fields. For example, an ecologist is obliged to know a good bit about taxonomy, and some of his work might very well involve still other fields such as anatomy and genetics. Also, fields which are purely morphological in approach may sometimes employ physiological techniques, and vice versa. An anatomist, for instance, might be interested in the overall structure of some animal or animal group. In order to learn the significance of an organ or part of a given animal, he might very well be driven to study its development and perhaps even the physiological activities of the part in question. Again, biochemistry and biophysics are applicable at every level of organization, and it should not be thought that they are restricted in scope to an isolated, subcellular area.

In spite of a certain amount of overlapping, however, the modern biologist is obliged to specialize in one branch or another of his science. This is because biological knowledge is now so vast that no individual can hope to keep abreast of all developments. Of course, there are certain fundamental principles which unify the several fields of biology, and we shall attempt to learn some of the more important of these principles.

- Summary**
- 1.3** Biology is the science of organisms. As one of the natural sciences, it is restricted to those phenomena which are subject to observation and experimentation. Three basic assumptions are made by scientists in studying or interpreting natural phenomena. These may be abbreviated by the key terms (1) observable phenomena, (2) uniformity, and (3) probability. Although there is no rigid pattern or scientific

"method" through which scientists work, several key terms are important in defining their activities. Some of these are hypothesis, theory, principle, control, and data.

The field of biology includes a great many subfields, each of which is concerned with a particular viewpoint. Some of the more important of these fields are anatomy, histology, taxonomy, paleontology, physiology, cytology, embryology, genetics, evolution, and ecology, as well as such areas as bacteriology and ichthyology. Many of these fields overlap, so that they cannot be separated from one another in an absolute sense.

Questions

1 Assuming that you are taking a course in introductory college biology as a requirement, why do you suppose your college requires it—especially since you probably had a course in high-school biology?

2 Distinguish between the terms hypothesis, theory, principle, and law. Why do you suppose many scientists object to the term "law" as it is frequently used in science?

3 What is meant by a *control* in experimental work? Although Pasteur had no stated control in that portion of his work presented in this chapter, what really constituted his control?

4 A college student once objected to taking required science courses because he was under the impression that scientists do not believe in God. To what extent, if any, was he justified in assuming this viewpoint?

5 Kemeny (see reference) states that "scientists spend their entire lives trying to get a small part of tomorrow's newspaper." What do you suppose he means?

6 Outline the fields of biology which were presented in this chapter and define each.

7 Suppose a person is driving an automobile and it suddenly stops. He proposes one hypothesis after another until he finds the cause. In terms of Conant's definition, is this science? What is the difference between technology and science?

8 As a library exercise, see if you can locate an essay by Abraham Flexner entitled "The Usefulness of Useless Knowledge." Now several years old, it is a highly eloquent statement of one aspect of science. It might also help you to answer Question 7, above.

References

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Matter, energy, and living systems

2

Living systems represent a highly organized state of energy and matter. As one surveys the history of man's attempts to solve the "mystery of life," it becomes apparent that a direct correlation exists between the concepts formulated and the development of techniques which have made it possible to study life at progressively lower levels of organization. The whole process is somewhat like opening a whole series of boxes-within-boxes. With the opening of each box, something more is learned about the nature of the entire package—if only the fact that yet another box remains to be opened.

To a great extent, the study of life has been, and continues to be, a matter of opening still smaller boxes. New concepts are formulated at each level of organization, and every new concept becomes fruitful (remember Conant's definition of science?) of still other conceptual schemes. Because modern biology has reached a point at which it is opening exceedingly small boxes (that is, at levels involving basic material and energetic units), it is necessary that the student of biology know something of the nature of matter and energy. Without these concepts, it is impossible to appreciate modern biology as a rapidly advancing experimental science.

2.1

The nature of matter and energy

Chemistry and physics have found it useful, for their purposes, to conceive of matter and energy in rather technical terms. Such conceptions must take into account the interconversion of matter and energy, and as a result, it is not always meaningful in these sciences to formulate a precise distinction between them. In living systems, it appears that there is very little interconversion between matter and energy (such as occurs, for example, when an atomic bomb is set off), and for this reason, we shall consider them as separate and distinct things. Whether they really are different does not concern us at this point, in fact, such a consideration lies in the realm of theoretical physics, and perhaps ultimately, in philosophy.

Matter The term *matter* is used to describe anything which occupies space and possesses mass. Thus, any definite object or substance within our material universe which can be apprehended by means of our senses or by instruments comes under this definition, whether living or nonliving. The term *substance* is used to describe matter which is uniform throughout, such as sugar, copper, water, and so on. From the negative standpoint, materials such as milk, dirt, air, and wood are *not* substances, because each is composed of several different kinds of matter.

Matter may exist as a *solid*, a *liquid*, or a *gas*. It is possible to convert most substances from one of these states to either of the others by the addition or subtraction of heat. Water, for instance, can be made to take the form of ice (a solid) or steam (a gas) by this means. Such a change does not alter the fundamental composition

of water: it only alters its *physical state*. Hence, such a change is called a *physical change*. However, if water were subjected to some process by which it could be made to combine with some other substance or to separate into its component parts (hydrogen and oxygen), such alteration of fundamental composition would be termed a *chemical change*.

Chemists and physicists, using a variety of substances, have investigated chemical changes exhaustively and have concluded that matter consists of certain fundamental particles called *atoms*. For purposes of present definition, an atom may be considered the smallest unit of matter which can enter into chemical changes. Just how large is an atom? Exact methods of computation indicate an almost unbelievable degree of smallness. It has been estimated that 100 million atoms arranged in a row would measure only an inch. Compared with the number of possible substances which exist, there are relatively few kinds of atoms. To be exact, physical scientists recognize the existence of only ninety-two naturally occurring kinds, although others have been produced artificially.

Let us suppose that we were able to obtain a substance made up of only one kind of atom. This would be an *elementary substance*, or as it is generally termed, an *element*, there being possible only ninety-two such substances in nature. Hence, an element is a substance composed of similar atoms. All these elements have been given names, some of which existed long before the particulate nature of the elements they represent was known. For purposes of brevity, there are symbols that represent each name. In the main, a symbol represents the first letter or the first and second letters of the English or Latin name of the element. For example, the symbol of the element phosphorus is P, that of calcium Ca, that of copper Cu, that of iron Fe, and so on. A complete list of the elements and their symbols can be found in any introductory textbook of chemistry.

Much evidence indicates that atoms are composed of three primary building blocks: *protons*, *neutrons*, and *electrons*. This is true of all atoms except that of hydrogen, which has no neutron. The protons and neutrons have almost 2,000 times the mass of an electron and are held together very tightly to form the compact *nucleus* of the atom. A proton has a positive electrical charge and a neutron is neutral (hence their names), which means that the nucleus has a net positive charge. The arrangement of protons and neutrons in the atomic nucleus is incompletely understood, as is the nature of the energy that binds them together. An electron has a negative electrical charge. The electrons of an atom move about the positively charged nucleus at varying distances from it, traveling at relatively high velocities. The number of electrons in an atom is ordinarily

equal to the number of protons, making the atom neutral with respect to electrical charge.

Variations in the numbers of protons, neutrons, and electrons which compose atoms account for differences in the elements they represent. Primarily, there are three ways of identifying an atom or the element to which it belongs. Probably the simplest and most orderly, at least for reference purposes, is to cite the *atomic number*. The atomic number of an atom is equal to the number of protons in the nucleus. This means that atomic numbers range from 1 for hydrogen, the simplest atom, to 92 for uranium, the most complex of the naturally occurring atoms. Atoms are also identified by *mass numbers*, in which case the protons and neutrons are considered to have a mass of one each, and the electrons are considered to have no mass. For example, carbon-12, which has six protons and six neutrons, has an atomic number of six and a mass number of twelve. As an element, it is frequently represented by the symbol ${}_6\text{C}^{12}$, in which case the subscript is the atomic number and the superscript is the mass number. A third means of identifying an atom, and one which is closely related to the concept of atomic mass, is that of *atomic weight*. Atomic weights of atoms are relative values determined by comparison of a given element with that of carbon-12. Thus the atomic weight of an element indicates whether it is lighter or heavier than carbon and by how much. For example, hydrogen (atomic weight 1.008) is approximately one-twelfth as heavy as carbon-12, and chlorine (atomic weight 35.453) is almost three times as heavy.

As recently as the year 1900, physical scientists assumed that the atoms composing a given element were identical. Because this assumption could not be reconciled with certain experimental data, however, special attention was given to the matter. It was soon learned that most elements are composed of two or more variant forms of atoms. The variant forms of a given element were named *isotopes*, and are atoms of the same element with the same atomic numbers but different mass numbers. In other words, they have the same number of protons and electrons, but not the same number of neutrons. For example, the element chlorine has two naturally occurring isotopic forms. One type of atom has a mass number of 35 (17 protons plus 18 neutrons) and the other type has a mass number of 37 (17 protons plus 20 neutrons). Precise analysis reveals that the proportions of these two isotopes in nature are about 75.4 percent of the lighter atoms (${}_{17}\text{Cl}^{35}$) to about 24.6 percent of the heavier atoms (${}_{17}\text{Cl}^{37}$). Consequently, the mass number averages out at 35.453. The atomic weight of a particular element, then, is defined as the average of the mass number values of all the naturally occurring isotopic forms of that particular element.

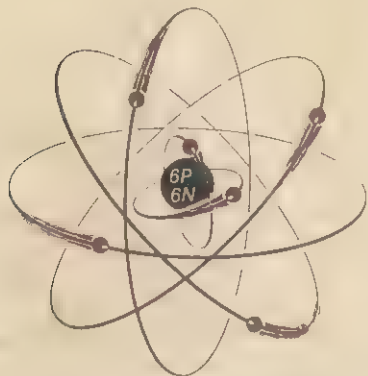


Figure 2.1 Theoretical structure of the carbon atom, whose six electrons occupy two separate shells around the nucleus. Both the electrons and the nucleus are greatly enlarged in terms of their actual sizes in relation to space within the atom.

The fact that most elements are isotopic is very fortunate for biology. For example, if an investigator wishes to trace the path of the element carbon in some living system, he may label some carbon compound with the relatively rare $^{14}_6\text{C}$ and determine its pathway or its ultimate fate by the use of instruments which are capable of detecting it. Within recent decades, isotopes have become widely used in biological research.

For our purposes, it is useful to view the atom as a miniature solar system in which the nucleus is analogous to the sun and the electrons to its planets (Figure 2.1).^{*} Thus, an atom consists more of space than of anything else. Actually, it is impossible to illustrate by means of a diagram just how much space really exists in an atom. To draw an analogy, suppose that an atom were expanded in size until it measured a mile in diameter. The nucleus would then be about twice the size of a baseball; the electrons, smaller than golf balls.

As we mentioned previously, electrons are located at varying distances from the nucleus, about which they travel at high velocities. We will have more to say about the behavior of electrons, since they become directly involved in chemical reactions. Before considering this aspect of matter, however, we need to understand some basic concepts regarding energy.

Energy In contrast to matter, energy neither occupies space nor possesses mass. Therefore, it cannot be defined from a material or structural viewpoint; it must instead be defined in operational terms, or in terms of its effect on matter. Energy is sometimes defined as the capacity to do work. Within this concept, it is useful to classify energy as either *potential* or *kinetic* energy. Potential energy is inactive or stored energy. It possesses the capacity to affect matter but it is not in the process of doing so. In contrast, kinetic energy is energy in action, that is, it is in the process of affecting matter. Figure 2.2 illustrates the difference in these two types of energy. In the system represented by Figure 2.2a, a certain amount of potential energy is present. As the boulder rolls down the hill (Figure 2.2b), this potential energy is converted to kinetic energy, and the amount released is approximately equal to the amount originally expended in getting the boulder to the top of the hill.

Energy may exist in a number of different forms. The most com-

^{*} This concept, which was proposed by Niels Bohr in 1913, has been generally accepted by physical scientists as a satisfactory elementary representation of atomic structure. Certain aspects of it, however, may not be valid. Whether neutrons, electrons, and protons are actually particles is a point of some debate. Furthermore, many other types of particles than those mentioned here are now recognized, and there are explanations of atomic structure which are technically more satisfactory than the Bohr theory. However, for purposes of simplification, this classical representation will serve better at this point, it is felt, than will any other.

Figure 2.2 (a) Potential energy represented by a boulder at the top of a hill. (b) Kinetic energy represented by a boulder in the process of rolling down a hill.



mon of these are thermal energy (heat), radiant energy (visible light, infrared and ultraviolet rays, X rays, gamma rays, cosmic rays), mechanical energy (as illustrated in Figure 2.2), electrical energy (the flow of electrons along a conductor), and chemical energy (energy possessed by chemical compounds). In both living and nonliving systems, energy is converted from one *type* to another (potential to kinetic and vice versa) and from one *form* to another (for example, from chemical energy to mechanical energy). We have only to consider a very common example of this conversion process to realize that it occurs. In an automobile engine, potential chemical energy is present in the form of gasoline. Upon its ignition by kinetic electrical energy, it is converted to kinetic thermal energy. This thermal energy is then partially converted to mechanical energy, which is eventually dissipated as heat, and so on (Figure 2.3).

As we shall see in a later chapter, these same types of conversions and transformations occur in living systems. Thus both living and nonliving systems demonstrate the *first law of thermodynamics*, which states that energy can neither be created nor destroyed but can simply be changed in form. Sometimes this generalization is called the *law of conservation of energy*. This concept is of considerable importance to biology, and we shall return to it.

One additional concept of energy which is basic to an understanding of chemical reactions in both living and nonliving systems is the *second law of thermodynamics*. As a concept, this law accounts for a multitude of complex phenomena, but stated simply, it holds that energy tends to dissipate itself. A good illustration of this may be seen in chemistry, where reactions proceed from high to low energy states. In other words, the second law relates energy changes in a system to the organization of that system. Placed in this context, it states that there is an increase in *entropy* (randomness)—that is, a decrease in organization. Since useful energy is organized energy, an increase in entropy means a decrease in useful energy.

How does this concept relate to the study of organisms? From one viewpoint, life itself might be regarded as a refutation of or an

exception to the second law of thermodynamics. If there is a tendency in an isolated system to proceed toward randomness, the implication is that energy must be taken constantly into a living system in order for it to maintain its organization. As a matter of fact, this is what actually occurs in living systems. The human body, for example, takes in potential chemical energy (food) which ultimately supplies kinetic chemical energy. These processes enable the body to maintain its organization, that is, it is prevented from wasting away. Thermodynamically, a living system is not qualitatively different from a nonliving system; the difference is a quantitative one, leading to increased complexity in the living system. Energy conversions in living systems are fantastically numerous and varied, but overall, enough energy is supplied from external sources to defer its progress toward randomness. When the supply of energy is insufficient, the organism dies, of course. In brief, although a living system may involve more than just physics and chemistry, we have no reason to believe that it demonstrates a physics and chemistry different from that of nonliving systems. Thus organisms exemplify not only the first and second laws of thermodynamics, but all other laws of physics and chemistry as well.

As we shall emphasize in a later chapter, the initial energy source for organisms is the sun. Green plants are capable of converting a portion of this radiant energy to kinetic and potential chemical energy. Animals and microorganisms then use these plants as a source of potential energy. At each step of energy transfer, there is a considerable loss. The energy lost, including the original radiant energy not utilized by green plants, goes on to a more disorganized state, that is, there is an overall increase in entropy. The universality of the second law of thermodynamics therefore hinges on

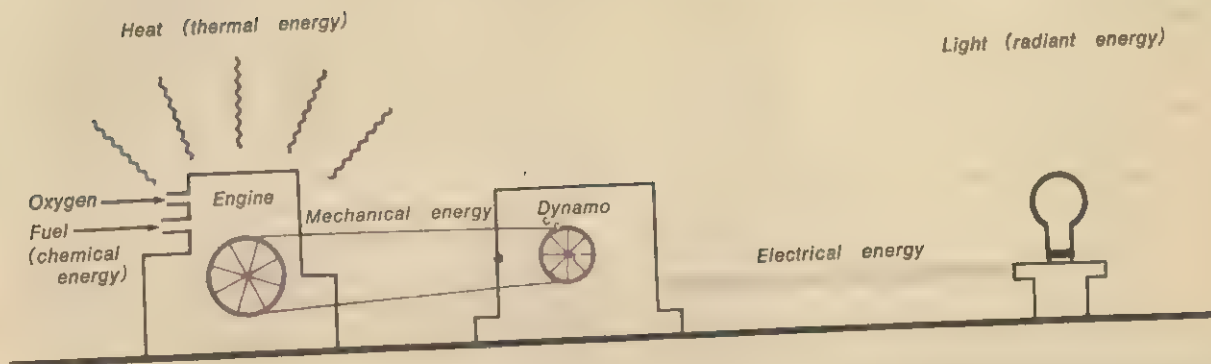


Figure 2.3 Some energy conversions, or transformations, from one type to another.

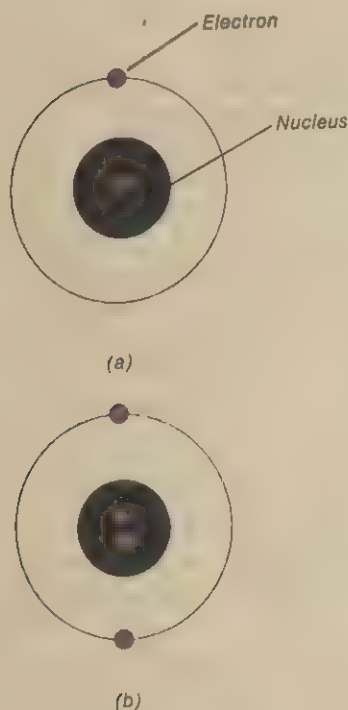


Figure 2.4 Two-dimensional representation of the hydrogen atom (a) and the helium atom (b). The nucleus of the hydrogen atom contains one proton and no neutrons; that of the helium atom contains two protons and two neutrons.

whether or not the balance sheet of the entire earth-sun system shows a decrease in free or usable energy. Many physicists feel that this is precisely the case, and they view the universe as analogous to a huge clock which was initially wound up and which will eventually unwind itself completely.

The matter-energy complex Armed with this brief and very simplified concept of energy, let us return to the nature of atomic structure. Previously, we depicted the atom as a miniature solar system in which the electrons travel about the nucleus (composed of protons and neutrons) in orbital fashion.

In order to understand the conditions which make possible the combination of atoms and the transfer of electrons to and from atoms, it is necessary to recognize that electrons do not revolve about the nucleus in a haphazard fashion. Rather, there are orbits, or "shells," which are restricted in the number of electrons each can contain. The simplest atom, that of hydrogen, is characterized by the presence of only one proton in the nucleus and one electron in orbit (Figure 2.4a). The helium atom possesses two protons and two neutrons in the nucleus and two electrons occupying the same shell (Figure 2.4b)

Experimental evidence indicates that the first shell surrounding the nucleus of an atom never contains more than two electrons. In the atom of lithium, for example, which possesses three protons in the nucleus and three electrons in orbit, two of these electrons orbit in the first shell and the third orbits in an outside shell. This second shell may contain as many as eight electrons. When more than ten electrons are present in the atom, a third shell is established outside the first two. This third shell may contain as many as eighteen electrons, the fourth shell thirty-two, the fifth shell thirty-two, the sixth shell eighteen, and the seventh shell two. However, not more than eight electrons are contained in whichever is the outermost shell of an atom.

The shells formed by orbiting electrons are not so much physical entities as they are energy levels. According to this concept, electrons may be viewed as units which possess certain amounts of potential energy, this amount in any particular case being determined by the energy level which the electron occupies in the atom. If we think of the nucleus with its net positive charge as attracting the negatively charged electrons with a certain force, then a theory can be presented in an effort to account for the electron-nucleus relationship: The farther the orbit (energy level) is from the nucleus, the more potential energy it represents. Perhaps an analogy will serve to clarify this theory. Imagine a cliff in which successively higher steps are cut, with rocks of equal size being placed in these steps. The

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higher the rock, the more potential energy it represents, because it required more kinetic energy to get it there in the first place. In this analogy, the steps represent different energy levels, or orbitals, and the rocks represent electrons. The analogy breaks down somewhat when we consider that electrons are in motion, but the principle is the same. However, because they are in motion, those electrons farthest from the nucleus can be removed from the influence of the nucleus more easily than those electrons situated closer to the nucleus. This is because the attracting force is inversely proportional to the square of the distance of the electron from the nucleus.

This concept of energy levels in the atom is basic to an understanding of the interaction of atoms to form molecules. It is also essential to an understanding of the energy transformations which occur in living systems, where electron shifts from one level to another within atoms are accompanied by a gain or loss in energy. As we shall see in a later chapter, these mechanisms account for the ability of green plants to "capture" the energy of sunlight, and they enable all organisms to make certain energy transformations within their cells.

2.2 The interaction of atoms

Thus far, we have considered only single atoms in our attempts to understand matter, and we have seen that energy is very much involved as a force within the atom itself. We will now concern ourselves with a higher level of organization of matter and energy, that is, particles which are composed of more than one atom. It is very important that we do so, because atoms generally do not exist singly, but are most often joined to other atoms to form *compounds*. In a compound, atoms are held together by an energy force called a chemical bond, which is somewhat analogous to a piece of elastic holding two balls together. Of course, the bond does not really consist of a material substance, but like a piece of elastic, it represents a certain amount of potential energy. To carry the analogy further, when either a piece of stretched elastic or a chemical bond is broken, potential energy is converted to kinetic energy. A chemical bond is apparently an energy relationship between atoms. The amount of energy in chemical bonds is variable and is dependent upon the number and kinds of atoms which are associated.

As we mentioned previously, the number of electrons in the outermost shell or energy level of an atom does not exceed eight, and in atoms that have more than one shell, the presence of eight electrons in the outermost shell represents stability. As a general rule, we can predict that atoms will interact to form compounds when all participants are able to achieve stability by doing so. In



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essence, we are saying that all chemical reactions involve an exchange of energy. This energy becomes kinetic as electrons interact in achieving stability, which means that bonds are either broken or formed, as the case may be.

For our purposes, there are two types of atomic interactions, based on the manner in which electrons of one atom relate to those of another atom. These are discussed separately below. In most cases, one of the atoms involved will be more or less positive than the other, and an electromagnetic attraction (the chemical bond) exists between them.

Ionic compounds Let us suppose that an atom has a second shell containing eight electrons, and that a single electron occupies a third shell. It has a tendency to give up this single electron in achieving stability, and it will do so under certain conditions to any atom which will accept the electron. In contrast, if we should find an atom with only seven electrons in its outermost shell, then it has a tendency to accept a single electron in achieving stability. If two such atoms are brought together, they make this exchange, and the result is an *ionic* or *electrovalent* bond. A number of similar interacting pairs of atoms comprise an ionic or electrovalent compound. For example, the sodium atom ($_{11}\text{Na}^{23}$) has eleven electrons, two of which form the first shell, eight of which form the second shell, while the remaining electron occupies a third shell. The chlorine atom ($_{17}\text{Cl}^{35}$), with seventeen electrons, has seven of these in its third shell. The chlorine atom readily accepts the outermost electron of sodium—this electron actually transfers to the chlorine atom. The resulting compound, sodium chloride, actually consists of two types of stable but electrically imbalanced atoms. An atom achieving structural stability through the loss or gain of electrons is called an *ion*. Hence, sodium chloride consists of two types of ions, the sodium ions and the chloride ions. These are represented by the symbols Na^+ and Cl^- , respectively, and the sodium chloride is represented by the formula Na^+Cl^- .

In such reactions as we have described, the total number of positive charges carried by one ion equals the total number of negative charges carried by the other. Since opposite charges attract each other we should expect that the positive and negative ions exert a mutual attraction. This force of attraction is termed the ionic or electrovalent bond. For example, in Figure 2.5, we have diagrammed the reaction $\text{Na} + \cdot\text{Cl} \rightarrow \text{Na}^+ \text{Cl}^-$; the end product is the ionic compound sodium chloride. In the compound, a single bond exists between the sodium ion and the chloride ion, formed by the electrical attraction these two ions have for each other. The reaction which

2.2 The interaction of atoms

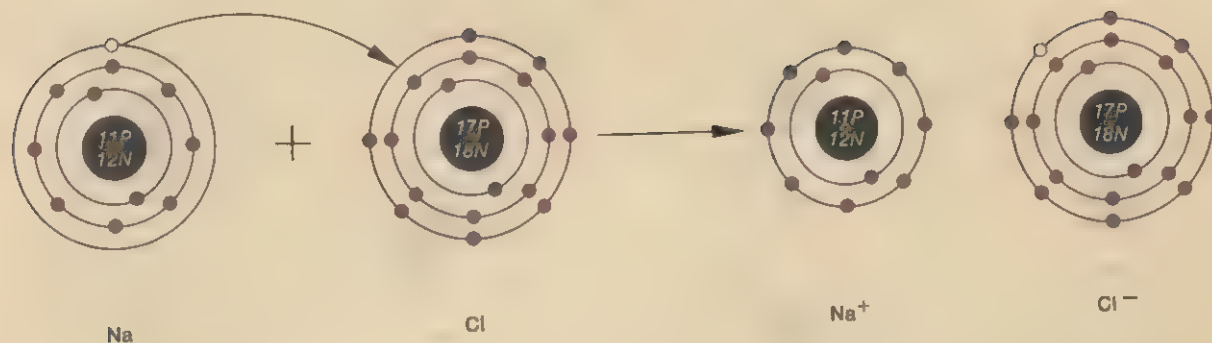


Figure 2.5 Electron transfer from sodium (Na) to chlorine (Cl), resulting in sodium and chloride ions.

resulted in this ionic situation is customarily called an *electron-transfer reaction*.*

Atoms do not always react in a one-to-one ratio in attaining stability. For example, consider the interaction between calcium (${}_{20}\text{Ca}^{40}$) and chlorine in the formation of calcium chloride ($\text{Ca}^{++}2\text{Cl}^-$). Let us remember that we can get a reaction between calcium and chlorine if all participating atoms achieve stability. This is accomplished quite readily in the interaction of calcium and chlorine, as shown in Figure 2.6. In other words, the calcium atom has two electrons to donate in achieving stability and, in a manner of speaking, it does not "care" whether it donates both electrons to a single atom or to a pair of atoms.

To summarize ionic or electrovalent interactions, it is meaningful to say that atoms with more than four electrons in the outermost shell have a tendency to accept additional electrons, whereas those with fewer than four tend to give them up, thus presenting a satisfied shell to the outside. From a purely physical standpoint, atoms which have interacted to form ionic bonds may be only loosely associated, especially if the compound they form is dissolved in some liquid such as water. This is in contrast to the generally closer physical relationship of atoms involved in the second type of interaction, presented below.

Covalent compounds Under certain conditions, atoms may satisfy their outermost orbits by sharing electrons. In this case, an energy

* In most cases, 100-percent ionization does not occur in ionic reactions, although the interaction of sodium and chlorine approaches it very closely. Electron transfer is usually incomplete, and the donated electron may occasionally circle the nucleus of the donor atom.

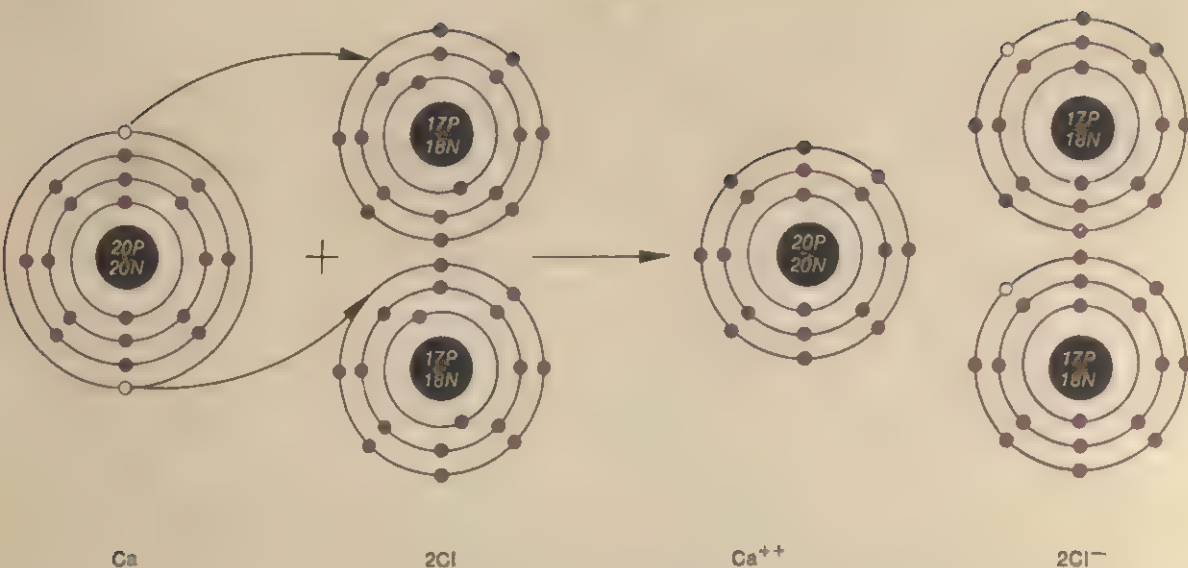


Figure 2.6 The interaction of calcium and chlorine in a 1:2 ratio. Compare with the interaction of sodium and chlorine, as shown in Figure 2.5.

bond is formed, and it is called a *covalent bond*. All atoms held together as a unit by covalent bonds are called a *molecule*.^{*} A compound which is composed of similar molecules is called a *covalent* or *molecular compound*. Using chlorine (${}_{17}\text{Cl}^{35}$) again as an example, let us consider how the atoms of this element might interact to achieve stability. Chlorine has seven electrons in its outer orbit, but eight are required for stability. Whenever a chlorine atom comes close to another chlorine atom, each "tries" to wrest an electron from the other. However, it is a drawn match, since each atom holds on to its electrons with equal tenacity. As a result, both atoms end up sharing a pair of electrons which sometimes circle the nucleus of one atom, and sometimes that of the other. By virtue of this arrangement, both atoms achieve stability, and comprise a molecule, which we symbolize as Cl_2 (Figure 2.7). Thus, chlorine does not exist naturally in the form of individual atoms but, rather, as molecular (Cl_2) chlorine. In similar fashion, many elements exist as molecules; for example, two hydrogen atoms interact to form a molecule of hydrogen (H_2).

^{*} Within molecules, especially those consisting of several types of atoms, one or more of the atoms may relate to the molecule ionically. As a result, a molecule may consist of atoms most of which are held together by covalent bonds, and some of which are related to others by ionic bonds.



Figure 2.7 The interaction of two atoms of chlorine in the formation of a molecule of chlorine.

Now let us consider the carbon atom (${}_6\text{C}^{12}$), which has four electrons in its outer shell. We might question whether it tends to give them up or take on four more in achieving stability. Actually, it usually does neither, but participates in the formation of molecules through a sharing of its electrons. Because of its outer shell configuration, carbon is a most versatile atom, and can form an almost infinite number of different arrangements with other atoms. For example, carbon reacts in the presence of hydrogen to form methane (Figure 2.8). In this case, each hydrogen atom shares a pair of electrons with the carbon atom.

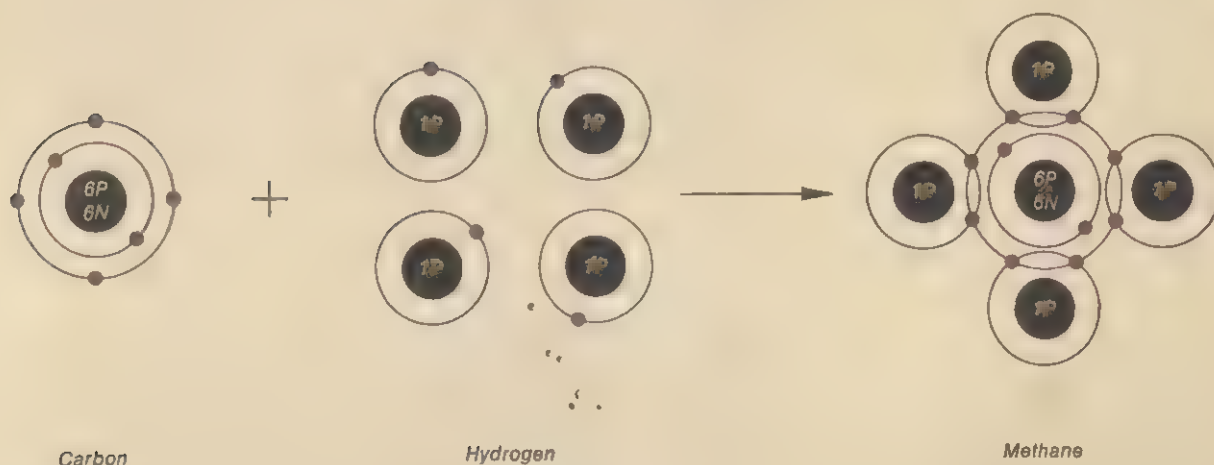
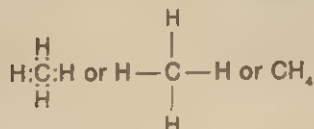
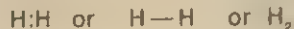


Figure 2.8 Formation of a molecule of methane by the combination of one carbon atom and four hydrogen atoms.

A number of ways may be used to present the relationship of shared electrons. For example,

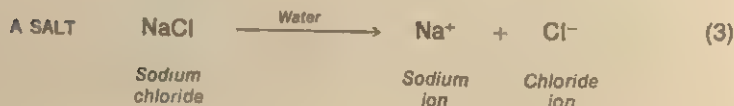
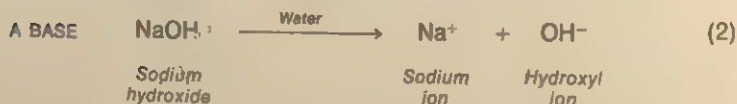
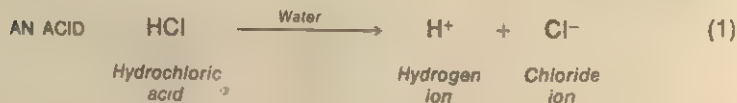


The most common method of representing molecular relationships is the second one shown above (especially for large molecules). Each line represents a pair of shared electrons, which form a chemical bond between the two atoms involved.

Ionic dissociation and electrolytes Water has been termed the universal solvent because it dissolves more substances found in nature than does any other known liquid. In living systems, practically all chemical reactions take place in an aqueous medium. For this reason, it is important that we understand some of the fundamental types of interactions between water and the compounds that go into aqueous solution.

Let us consider what happens when we mix a spoonful of sodium chloride with a pint of water. Not only does sodium chloride dissolve in water, but it also dissociates (ionizes), thus releasing Na^+ and Cl^- ions into the solution. Since there are equal numbers of positively and negatively charged ions, the solution remains electrically neutral. However, the very fact that there are ions of opposite charge in the water means that an electric current can pass through the solution. Thus compounds that ionize in water are known as *electrolytes*; and those which do not ionize in water are called *nonelectrolytes*.

Fundamentally, electrolytes fall into three groups known as acids, bases, and salts. Dissociation to form each type is as follows:



In Equation (1), hydrochloric acid dissociates and releases hydrogen ions into the water, and it is the presence of these hydrogen ions that makes the solution an acid. For our purposes, we may define an acid as any compound yielding hydrogen ions upon dissociation. In Equation (2), let us note that sodium hydroxide produces hydroxyl ions in its dissociation. We thus define a base as any substance yielding hydroxyl ions upon dissociation. Salts such as sodium chloride, shown in Equation (3), yield neither hydrogen nor hydroxyl ions in their dissociation. Furthermore, salts are usually formed by a chemical reaction between an acid and a base. For example:



There are more technical definitions of acids, bases, and salts than the ones we have given and the chemist is often obliged to formulate such definitions. However, these will serve us as beginning concepts, and in this book the terms will be used according to these definitions.

The strength of an electrolyte is determined by the degree to which it ionizes. For example, hydrochloric acid is a strong acid because it dissociates almost completely into hydrogen and chloride ions. In contrast, an organic acid such as acetic acid (CH_3COOH) is considered to be relatively weak because only a small percentage of its molecules dissociate into ion pairs ($\text{CH}_3\text{COO}^- + \text{H}^+$). Similarly, there are strong and weak bases and salts.

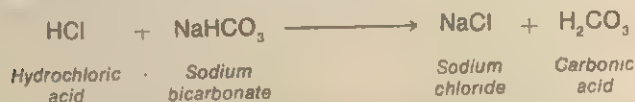
Hydrogen ion concentration and the role of buffers The hydrogen ion concentration ($[\text{H}^+]$) is extremely important to the structural and functional integrity of living systems. Even slight changes in $[\text{H}^+]$ may cause profound changes in the large molecules and molecular complexes composing organisms. The molecular balance in a living system is usually so delicate that even slight changes may be incompatible with life. Consequently, it is important that we understand something of the regulation of $[\text{H}^+]$ in living systems.

Hydrogen ion concentration is expressed in terms of *pH* units, representing a measure of the acidity or the alkalinity of a solution. The scale of pH units goes from 0 to 14. The midpoint of this scale is 7, the pH of pure water. Since this is where hydrogen and hydroxyl ions are equal in number, a pH of 7 represents neutrality, that is, a midpoint between acidity and alkalinity. Solutions with pH values of less than 7 have more hydrogen ions in the solution than hydroxyl ions, and those with pH values greater than 7 have more hydroxyl ions in solution than hydrogen ions.

The pH scale is not an arbitrary set of numbers. It is based on the

quantitative measurement of the number of hydrogen ions, which is one 10 millionth ($1/10,000,000$) of a gram, present in 1 liter of pure water. Since it is awkward to deal with numbers or fractions involving many zeros, it is much simpler to express the number given above exponentially as 10^{-7} . In turn, it is simpler to deal with whole numbers than with exponential numbers, and so the pH of water is expressed by the number 7. Similarly, solutions which have more or fewer hydrogen ions are expressed by numbers on the pH scale, and perhaps you can see why the pH value goes *down* as the $[H^+]$ goes *up*. In summary, the pH of a solution is the negative logarithm of its hydrogen ion concentration ($pH = -\log [H^+]$).

The body fluids of most organisms must be maintained at a point rather close to neutrality. In view of the fact that most organisms are frequently exposed to acids and bases of sufficient strength to alter the relatively constant pH values of their body fluids, there must be a way to maintain this constancy. Organisms do indeed possess a mechanism for the maintenance of a steady pH through the presence of compounds that form a buffering system. A buffering system usually consists of a weak acid (only slightly ionizing) and a salt which is chemically related to the acid. For example, sodium bicarbonate ($NaHCO_3$) and carbonic acid (H_2CO_3) constitute a buffering system, since carbonic acid is a weak acid and sodium bicarbonate is its salt. Let us suppose that a strong acid (such as hydrochloric acid) is added to this buffering system. In this case, we would expect the addition of such a flood of hydrogen ions to lower the pH drastically. Actually, it would do so, were it not for the buffering system. Instead, the following reaction takes place:



It will be noted that the hydrogen ions released by the ionization of hydrochloric acid are used to form carbonic acid, which ionizes only to a slight degree. Therefore, the $[H^+]$ is changed very little and the pH remains approximately the same. In other words, a strong acid is converted by a salt into a weak acid which is chemically related to the salt.

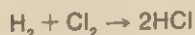
Living organisms possess buffering systems, without which pH constancy would not be possible. By virtue of these mechanisms, organisms are protected from the acids or bases in their environment, including those acids or bases which may be produced within living systems themselves. Of course, it is possible to add so much acid or base to a system that buffering agents are completely swamped. In this event, marked changes in pH will occur, and few

organisms can withstand more than a slight deviation from their characteristic pH.

2.3 Interaction between compounds In a previous section of this chapter we learned that, when atoms unite to form compounds, the atoms themselves achieve stability. It might be concluded from this that, when a compound is formed, it is stable and nonreactive. However, this is not necessarily the case. Under certain conditions of temperature, pressure, pH, or other factors, compounds may undergo alteration or may interact with other compounds. This involves breaking existing bonds and the formation of new ones. We have already seen how this may occur whenever acids or bases react with buffering systems, or even with one another. However, let us now look more closely at chemical reactions—the breaking of old bonds and the formation of new ones.

Basic types of chemical reaction By way of analogy, let us consider atoms as letters, molecules as words, and a chemical reaction as a sentence imparting a thought. Just as there are ways to classify sentences, so we may deal with chemical reactions according to type. For our purposes, the five types of reactions listed below are fundamental ones.

Synthetic reactions As the name implies, something is made in a reaction of this type. For example,



Since two substances react to form a third, we might represent this reaction abstractly as follows:



Synthetic reactions are quite common in living systems. For example, many of the reactions involved in growth, where new substances are being formed constantly, are synthetic in nature.

Decomposition reactions This type of reaction is the reverse of a synthetic reaction. To illustrate,



As we would suppose, a decomposition reaction may be represented symbolically as



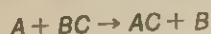
Decomposition reactions are also quite common in living systems, particularly in such processes as digestion and respiration, where complex molecules are broken down into smaller molecules.

Displacement, or exchange, reactions Displacement reactions

involve the replacement of an atom or a group of atoms by another atom or another group. Let us consider the following typical reaction:

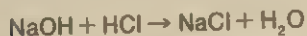


This type of reaction may be generalized as follows:



Displacement reactions are very important to living systems. For example, in the body fluids of higher animals, various ions and molecules constantly displace each other as they are transported to and from tissues by certain compounds.

Double displacement reactions These reactions involve a mutual exchange between compounds. For example,

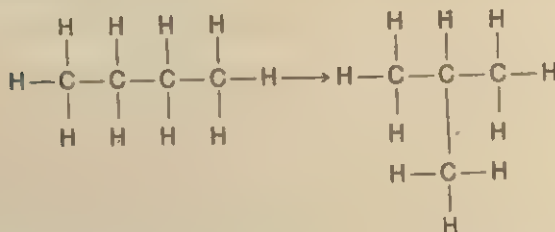


This reaction may be symbolized as follows:



Double displacement reactions are quite common in living systems. Buffering reactions (already discussed) are included in this type.

Rearrangement reactions These reactions simply involve a change in the bonding pattern within a molecule where there is no change in the number or kinds of atoms. This may be shown by the following:



This reaction may be represented symbolically as shown by the following equation:



Rearrangements of this sort are very common in living systems, especially in the breakdown of food molecules. For example, certain sugars are rearranged to form others without any quantitative change. There is simply a rearrangement of atoms within the molecule.

The relation
of energy
to chemical
reactions

2.4 Although a simple classification of chemical reactions such as that given above is useful, it provides little insight into the underlying mechanisms by which reactions are initiated and carried on. It takes additional insight, for example, to predict what reaction will occur, the rate at which a given reaction will proceed, or whether a reaction will go to the left (as we symbolize reactions) or to the right. Certainly, it is beyond the scope of this book to attempt a thorough treatment of chemical energetics, but perhaps we can gain an understanding of a few elementary concepts.

Energy exchanges All chemical reactions involve the exchange of energy. You will recall that compounds are made up of atoms which are held together by energy forces called chemical bonds. The amount of residual energy in compounds is variable, of course, but we must conceive of a compound as a reservoir of energy. You will also recall that the second law of thermodynamics implies that a closed system (one in which there is no input of energy) is a losing proposition, from an energy viewpoint. In other words, there is a decrease in total energy content (*enthalpy*) and organization, or we sometimes say that there is an increase in randomness (*entropy*). Since chemical reactions involve the exchange of energy, a closed chemical reaction displays this tendency. We might say that it exemplifies the second law. In any given chemical reaction, the state of the participating compounds which represents the lowest enthalpy (designated H) and the highest entropy (designated S) is the stablest form of that reaction. In a closed system (provided the reaction gets started) it will proceed in the direction of greatest stability. Thus, chemical reactions may be predicted on the basis of energy relationships. In actual practice, reactions are characterized by the changes in H and S . These changes in total energy and in organization are symbolized by Δ (delta) H and ΔS , respectively.

More precisely, chemical reactions are usually characterized in relation to energy changes by considering the amount of free energy which results from the reaction. By free energy, we mean energy available for doing useful work, and we symbolize it as F . The change in free energy resulting from a chemical reaction would then be symbolized as ΔF . This amount of free energy can be determined by considering the ΔH and ΔS that were introduced above. For example, consider the following generalized reaction:

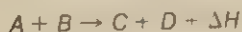


If H (total energy) represented by A and B on the left side of the equation is greater than H represented by C and D on the right side,

then the reaction will proceed readily from left to right, inasmuch as *C* and *D* represent a more stable condition. In this case, energy will be lost to the environment so that the total energy change (ΔH) is negative, that is, it is lost from the system. In consideration of the energetics involved, the reaction may be written as follows:



If the converse were true, then energy would have to be supplied from some external source and the reaction would be



Now consider *S* (entropy) and ΔS (change in entropy). If ΔH is zero in the reaction immediately above, which means that there is no change in total energy in the reaction, and if energy is equally distributed between *C* and *D* on the right but unequally distributed between *A* and *B* on the left, there is a difference in *S*. The left side of the equation would thus represent more organization, or less entropy (*S*), and the right side would represent a higher *S*. Left to itself, the reaction would tend to go from left to right, since a high *S* represents greater stability. It would then be written as follows:



If the converse were true, the equation would be written as follows:



In this situation, of course, energy would have to be supplied in order for the reaction to occur, since reactions tend toward randomness if they are completely closed.

To view the matter from a different standpoint, entropy is a function of temperature. To illustrate, let us consider the physical states of water, that is, its existence as a solid (ice), a liquid (water), or a gas (steam or vapor). Steam is the least organized state of the three, whereas ice represents the greatest state of organization. Since the physical states of water are temperature-dependent, then temperature must be considered in determining changes in entropy from one state to another. The mathematical expression used is a product of temperature (*T*) and entropy change (ΔS), or $T\Delta S$.

Free energy is a function of both enthalpy (*H*) and entropy (*S*). Energy which goes to randomness is lost as far as useful work is concerned. Therefore, we may express the following relationship:

$$F = H - TS$$

Free energy Enthalpy Temperature-
dependent entropy

Stability changes in a chemical reaction are also dependent upon H and TS , which are variables. As enthalpy decreases, stability increases. However, the very reverse is true of entropy. As entropy decreases, stability decreases. In other words, changes in stability are *inversely* proportional to changes in enthalpy and *directly* proportional to changes in entropy.

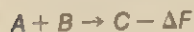
Perhaps we are now ready to express the second law of thermodynamics symbolically in terms of free energy changes, as shown in the following equation:

$$\Delta F = \Delta H - T\Delta S$$

Free energy change
Total energy change
Change in temperature-dependent entropy

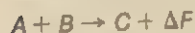
It should be obvious from the discussion presented above that reactions exhibiting a negative free energy change ($-\Delta F$) result in a more stable condition, and that reactions exhibiting a positive free energy change result in a less stable condition.

Now let us consider the following generalized reaction:



This means that in the reaction free energy is lost from the system to the environment. Consequently, the reaction will proceed in the direction of C , which represents the greatest stability with reference to this system. Such a reaction is called an *exergonic* reaction.

Now consider this reaction:



In order for this reaction to take place, energy will have to be supplied from the environment to the system. In this reaction C represents a less stable condition than $A + B$. Such a reaction is termed an *endergonic* reaction.

It is generally true that in a living system decomposition reactions (those in which compounds are being broken down) are exergonic, characterized by $-\Delta F$, while synthetic reactions (those in which compounds are being built up) are endergonic, characterized by $+\Delta F$. In a living system, metabolism (the total of chemical activities) is so ordered that the exergonic reactions are coupled to the endergonic reactions, thus supplying the necessary energy for uphill synthetic processes.

Perhaps this explanation of energy relationships in chemical reactions seems unduly complex, and indeed, it is not an easy subject. We shall find these concepts extremely useful, however, in understanding many of the life processes which we will encounter in later chapters.

Activation energy and catalysis Regardless of whether a particular chemical reaction is exergonic or endergonic once it gets started, there may be an energy barrier to overcome in starting the reaction. In such an event, a certain amount of energy must be supplied to the reaction initially, and this is termed activation energy. Although little or no activation energy is necessary in the case of some reactions, those of biological importance usually require considerable amounts. This is especially true if the reaction is to occur at a biologically significant rate.

In order for a chemical reaction to take place the reactants must come together, or collide. In the case of large molecules, reactive sites may be restricted to a relatively small area of the molecule, in which case the collisions have to be quite precise. In addition, the collisions may have to be of sufficient force to overcome the initial repulsions of electrons surrounding the atoms of the interacting molecules. These are some of the reasons why activation energy is usually required in a reaction.

This is precisely the reason that a Bunsen burner is standard equipment for the student in chemistry. In many cases, if two compounds are mixed together in a common solution with the expectation (based on the thermodynamic principles we have just discussed) that they will react, they do so not simply because they are brought together. Even if there is a reaction, it may proceed at such a slow pace as to be imperceptible. However, when heat is applied, the reaction proceeds very rapidly. In this case, the heat serves as the energy of activation and enables the system (that is, the reactants in solution) to overcome the initial energy barrier. It accomplishes this by increasing the rate of movement of reacting molecules, thus increasing their chances for collision. It also increases the force of collision, thus enabling one reacting molecule to overcome any existing repulsion caused by the electrons of the other reacting molecule.

If such a reaction as that just described is exergonic ($-\Delta F$) the excess energy given off may be sufficient to keep the reaction going. This is analogous to starting a small gasoline engine with a pull cord. Once the initial energy is supplied, it manufactures its own spark, and the "reaction" is self-perpetuating. In contrast, if the reaction is endergonic ($+\Delta F$), a continuous source of energy will have to be supplied as reaction energy. This is somewhat like using a large engine whose total energy output is utilized for manufacturing some product, and whose "spark" must be supplied from an outside power source. To look at it another way, exergonic reactions go downhill once they get started, but there is an initial "hump" to



Figure 2.9 A contrast of endergonic and exergonic reactions from an energetic viewpoint. In each case, a reaction must be supplied with activation energy. An endergonic reaction continues uphill and thus requires energy. In contrast, an exergonic reaction (once it gets over the activation hump) proceeds on its own.

overcome. In contrast, endergonic reactions are uphill all the way (Figure 2.9).

In principle, living systems are so organized that excess energy from exergonic reactions supplies both the activation energy and reaction energy for endergonic reactions. In applying this principle to living systems, however, one immediately encounters a high degree of complexity that demands a number of qualifications. Although we shall deal with some of these in a later chapter, there is one qualification that deserves attention at this point.

In the example of activation energy given above, heat was employed to give the exergonic reaction its initial push. However, a living system must operate, in most cases, within a rather narrow temperature range. The amount of heat required to serve as activation and reaction energy for many vital chemical reactions would completely destroy the living system. For this reason, we should expect to find some alternative mechanism for supplying activation energy. Such a mechanism does indeed exist in living systems in the form of substances called *catalysts*. Catalysts are substances which alter the rates of chemical reactions without being changed themselves in the process. They vary in structural complexity from simple

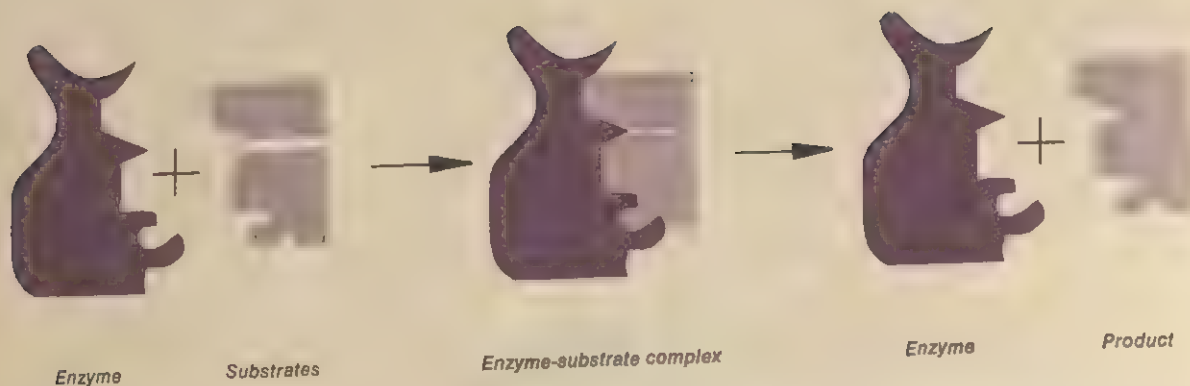


Figure 2.10 Diagrammatic representation of an enzyme-substrate reaction. According to this concept, the enzyme is geometrically specific for these two substrate molecules, which are combined into a single product molecule. The enzyme remains unchanged at the end and may be involved over and over in identical reactions. The reaction illustrated is a synthetic reaction. How would you alter the diagram to show decomposition and rearrangement reactions?

ions to extremely large and complex molecules. The catalysts which are of greatest interest to us are called *enzymes*, and by chemical definition, they are protein molecules of considerable size and complexity. We shall defer a discussion of proteins to a later section of this chapter, but at this point, let us note a few characteristics of enzymes.

First of all, enzymes exhibit a high degree of specificity, that is, a given enzyme is able to catalyze only one type of reaction or, at the most, a few related types. To draw an analogy, it is like a key which is specific for only one lock or one class of locks. Actually, this is probably a valid analogy in a structural sense as well as a metaphorical one. It appears that a given enzyme has a certain geometrical surface configuration on one part of the molecule into which only certain reactants fit. In an enzymatic reaction, the reactants are called *substrates*. The enzyme-substrate relationship is therefore very much like a key-lock relationship. When lock and key (substrate and enzyme) come into intimate contact, the substrate or substrates are altered in a highly specific manner (Figure 2.10).

Experimental evidence indicates that an enzyme first combines with a substrate or substrates to form an enzyme-substrate complex. Subsequently, the product or products of the reaction are released, and the enzyme molecule leaves the reaction in its original form. Thus, it can be used to catalyze the same reaction again, and it may serve millions of times before finally "wearing out." An enzymatic reaction can be illustrated symbolically as follows:



This is an example of a *synthetic* reaction, with *A* and *B* combining to form (synthesize) the product *AB*. This is the type of reaction illustrated in Figure 2.10. In some cases the enzyme forms a complex with only one substrate and the reaction yields two products, in which case we speak of a *decomposition* reaction. A third type of enzymatic reaction is one in which the product is simply a rearranged substrate molecule. In this case, we speak of a *rearrangement* reaction.

As we mentioned previously, the amount of heat ordinarily required to serve as activation energy for chemical reactions is incompatible with living systems. It appears that the chief function of enzymes, from a thermodynamic standpoint, is that of reducing the thermal energy of activation to a minimum. Instead of increasing the rate of movement of reactant molecules, the enzyme molecule offers a specific surface onto which the reactant molecules fit. Drawing upon our former analogy again, a locked door could be opened by melting the lock with a blowtorch, but this would ruin the whole door—it is much more efficient to use a key.

There are many aspects of enzyme activity other than those related to specificity, and we have concentrated on this particular characteristic because it points up some of the difficulties inherent in studying reactions which occur in living systems. We are obliged to merely mention in passing that enzymatic activity is temperature- and pH-dependent, and that the direction, rate, and duration of enzymatic reactions depend primarily upon the concentration of enzymes and/or substrates, as well as upon the energy relationships which exist between substrates and products.

2.5 Basic molecules of living systems For many years, it was supposed that living organisms were characterized by the presence of compounds fundamentally different from those found in matter not part of a living system. Many such compounds known to associate only with living organisms were called *organic* compounds, all others being designated as *inorganic* compounds.

Although it is still a good rule to associate organic compounds with organisms and their chemical activities in biology, the original distinction is no longer valid in chemistry. To qualify according to present-day general usage, a compound need only be characterized by having one or more carbon atoms in its molecules to be considered organic, with the exception that one group of carbon compounds, the carbonates, are classed as inorganic. Thus many organic compounds are known which are never associated with living

organisms at all. In fact, thousands of such compounds which do not occur naturally have been synthesized in the laboratory. Furthermore, many inorganic compounds are quite closely associated with living systems, as will be made apparent in later chapters. Nevertheless, organic compounds, other than those which are produced synthetically in the laboratory, are the products of living systems. Thus, the original distinction is valid to a degree.

It should be pointed out that carbon is something of a fundamental element of living matter. Its covalence (4) permits carbon to attach to various atoms and groups of atoms in a large number of different combinations. The relatively low potential energy of the carbon-carbon bond makes it possible for carbon atoms to form chains of almost unlimited length.* The number of carbon compounds known today exceeds all others, indicating something of its versatility.

A vast array of organic molecules is found in living systems, and these may be classified in a number of ways. However, for our purposes, we will emphasize four basic types: *carbohydrates*, *lipids*, *proteins*, and *nucleic acids*. Because of their importance to living systems, they might be called the basic molecules of life.

Fundamentally, activities in a living system center around the synthesis of large molecules (*macromolecules*†) from small ones (*micromolecules*), and the decomposition of macromolecules to micromolecules (Figure 2.11). Most of the molecules involved in these activities belong to the four listed types, and are discussed separately below.

Carbohydrates As the name carbohydrate implies, these compounds contain the elements carbon, hydrogen and oxygen according to the general formula $(CH_2O)_n$, where n may be any number. The carbohydrates are extremely important components of living matter. In addition to constituting the major fuel substances (sources of energy) in living systems, they play an important structural role, especially in plants.

Although there are carbohydrates whose molecules contain three, four, or five carbon atoms, the most common micromolecules are the six-carbon sugars called *monosaccharides*. It is from these six-carbon micromolecules that the complex macromolecules (*poly-*

* Paradoxical as it might seem, a chemical bond representing relatively little potential energy is very strong, whereas one which we call a high-energy bond is relatively weak. Can you advance a possible explanation for this?

† The term macromolecule is usually restricted to the extremely complex protein and nucleic acid molecules. We shall use it in a more general sense to describe a molecule which may be decomposed into several smaller units. We shall apply the term micromolecule to such units as are produced in decomposition, or which may be "multiplied" in synthesis to form macromolecules.

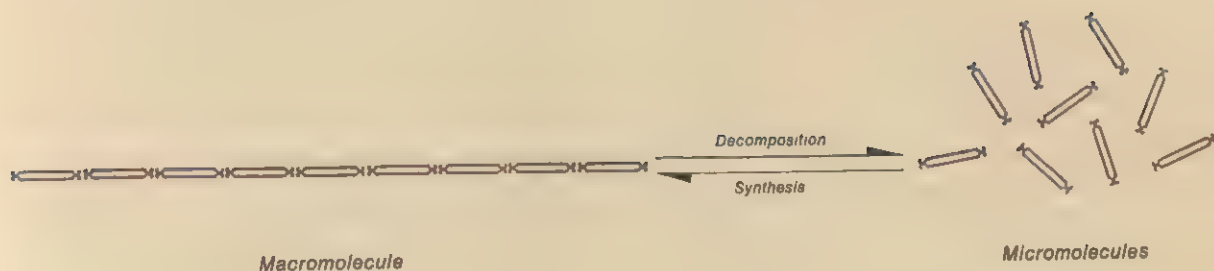


Figure 2.11 A diagrammatic representation of decompositional and synthetic reactions characteristic of living systems.

saccharides) are built. Conversely, in a living system, the large polysaccharides must be broken down into the smaller monosaccharides in order to be utilized.

In the process of building the macromolecular polysaccharides from the micromolecular monosaccharides, and in the decomposition of polysaccharides to monosaccharides, intermediate carbohydrate units called *oligosaccharides*, *trisaccharides*, and *disaccharides* are formed. The prefix *oligo* means "a few" and describes a carbohydrate containing few or several monosaccharide units joined together. The prefixes *tri-* and *di-* refer to three and two, respectively. From the standpoint of increasing complexity, therefore, we may classify carbohydrates as monosaccharides, disaccharides, oligosaccharides, and polysaccharides.

The names of the simpler carbohydrates end in *-ose* and they

either contain an *aldehyde* ($\text{R}-\text{C}\begin{smallmatrix} \text{O} \\ \parallel \\ \text{H} \end{smallmatrix}$) structure or a *ketone* ($\begin{smallmatrix} \text{R} \\ \diagdown \\ \text{C}=\text{O} \\ \diagup \\ \text{R} \end{smallmatrix}$)

structure, in which case they are called *aldoses* or *ketoses*, respectively. The number of carbon atoms in the molecule is sometimes designated by a prefix. Thus, a simple carbohydrate containing four carbon atoms is called a *tetrose*, one with five a *pentose*, and one with six a *hexose*.

Among the monosaccharides are the biochemically important compounds glucose, fructose, galactose, and ribose (Figure 2.12). As shown by their structural formulas, glucose, fructose, and galactose are *hexoses* (six-carbon chain), whereas ribose is a *pentose* (five-carbon chain). Notice also that glucose, galactose, and ribose are *aldoses*, whereas fructose is a *ketose*.

Glucose is by far the most abundant monosaccharide in nature, that is, it is the most common micromolecular carbohydrate unit

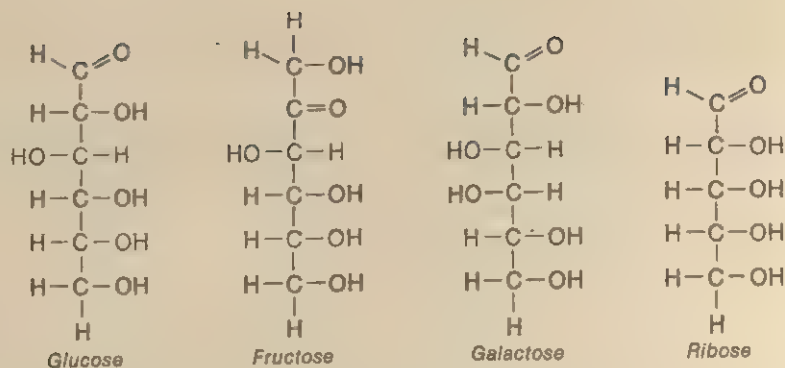


Figure 2.12 Open-chain structural formulas of four monosaccharides commonly found in living systems.

used as fuel by living cells. Fructose and galactose may also be used as fuel for cells; in fact, when glucose is broken down in living systems, it is changed to a form of fructose. In addition to its function as a fuel substance, ribose is one constituent of the nucleic acids, which we will discuss later.

Because of the relative importance of glucose to living systems, let us use it to illustrate the manner in which micromolecular carbohydrate units are linked together to form di-, tri-, oligo-, and polysaccharide carbohydrate structures. It should be understood, of course, that other micromolecules may be involved in a similar fashion.

In Figure 2.12 the glucose molecule is illustrated as a straight or open chain. Actually, evidence indicates that it exists primarily as a cyclic or ring structure as shown in Figure 2.13a. Notice that carbons 1 and 5 are connected to either side of an oxygen atom, thus forming a five-membered ring (pyranose form). A more convenient and realistic way of illustrating glucose is shown in Figure 2.13b, where the pyranose ring can be seen more clearly.

Under certain conditions, two glucose units may bond together to form the disaccharide maltose, as shown in Figure 2.14. Notice that in this figure water is shown as being removed during the reaction and adjacent carbons (1 and 4) are bonded by an oxygen atom. In similar fashion, another glucose unit may be added to form a trisaccharide. The addition of still others would form an oligosaccharide, and finally, a large macromolecular polysaccharide would result. This very process occurs in many animals when the polysaccharide glycogen is formed and stored; in plants, the multiplication of glucose units produces starch as a polysaccharide. A reversal of the process just illustrated results in the breakdown of glycogen and starch to their component glucose molecules. This occurs in plant and animal digestion, for example, when the 1-4 carbon linkages are

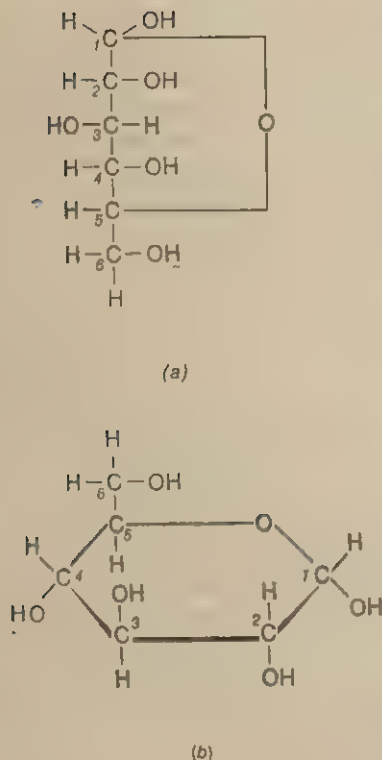


Figure 2.13 Two representations of the ring-form structure of the glucose molecule. For reference purposes, carbon atoms are numbered in order.

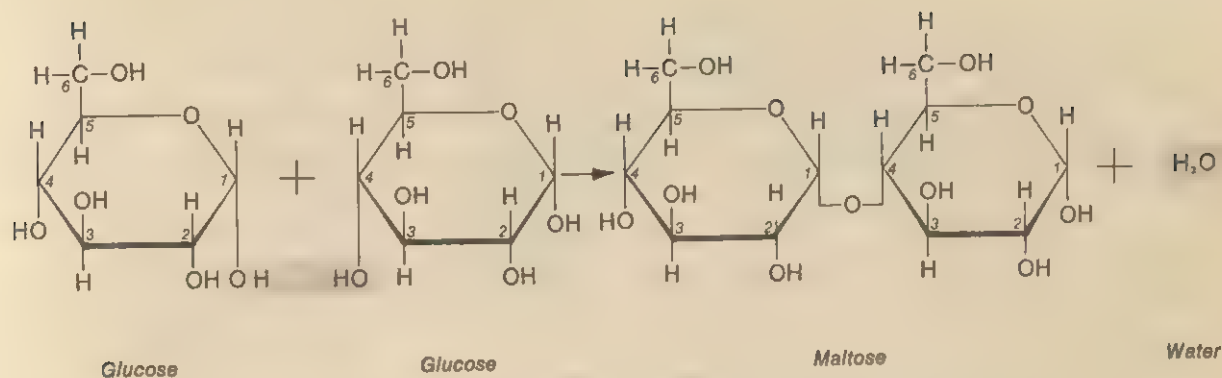


Figure 2.14 The combination of two glucose molecules in the formation of maltose, a disaccharide. In this representation, carbon atoms 1 through 5 are not drawn, although their respective locations are indicated by number.

broken through enzymatic action and a molecule of water is split ($H + OH$) and added to each linkage site. Reactions involving a breakage of bonds with the addition of water are called *hydrolytic reactions*.

Lipids Lipids are a very diverse group of organic substances which are classified together because they are all soluble in such fat solvents as ether and chloroform. As a rule, they are insoluble in water. The lipids are generally classified into three main groups, as follows: (1) simple lipids (fats and waxes), (2) compound lipids (glycolipids and phospholipids), and (3) steroids.

In order to gain some insight into the nature of lipids, let us concentrate briefly upon one of the simpler types, the fats. As is the case with so many of the biologically important organic compounds, fats are macromolecular complexes composed of smaller micromolecules, or building blocks. Specifically, a fat molecule is composed of the three-carbon micromolecule glycerol, to which are attached three fatty acids of varying length. Figure 2.15 shows the structure of a common animal fat, tristearin, which is formed by the combination of three molecules of stearic acid, a fatty acid, with one molecule of glycerol. As Figure 2.15 shows, the hydrogens from the three alcohol ($-CH_2OH$) groups of the glycerol molecule break off

with the hydroxyl (OH) radical from the three acid groups ($-C(=O)OH$)

of the stearic acid to form three molecules of water, thus leaving the adjacent carbons bonded together by oxygen. This type of linkage

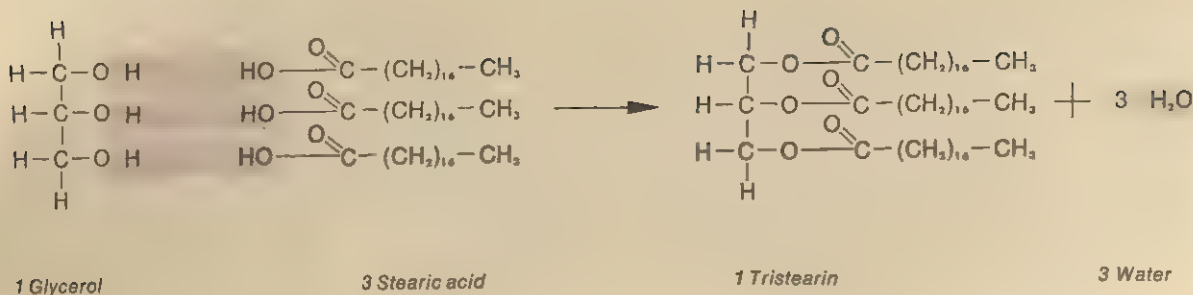
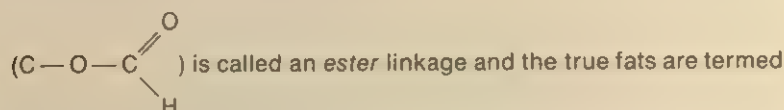


Figure 2.15 Synthesis of the animal fat tristearin from glycerol and stearic acid



glycerol esters or triglycerides.

Fats are quite common in the bodies of animals and are found to a lesser degree in plants. They represent stored energy, and gram for gram, they yield the most energy of any foodstuff. Stored fats are broken down by a reversal of the process shown in Figure 2.15. By this means, fatty acids and glycerol are made available to the body as fuel substances. This breakdown also occurs in the digestion of fats. As a process, it involves the addition of water at existing ester linkages, which are broken in the process. In other words, the breakdown of fats, like that of macromolecular carbohydrates, is hydrolytic.

The waxes, which we shall mention only in passing, are similar to the fats in that they are fatty acid esters. However, instead of being esters of glycerol, they are esters of long-chain alcohols. They are found as protective coatings on the skins and furs of animals and on the leaves and fruits of plants.

The compound lipids (glycolipids and phospholipids) are important structural compounds in living systems. Chemical analysis and electron microscope studies strongly indicate that a double layer of phospholipids makes up a large part of the membranes of cells. In addition, they are thought to play a role in a number of metabolic processes including fat metabolism, respiration, and enzyme activation. The glycolipids are quite common in certain nervous tissues of the more complex animals.

The steroids are chemically related to the triglycerides and compound lipids, although their molecular structure is quite different from that of other lipids. They are classified as lipids primarily because of

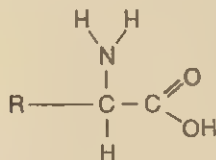


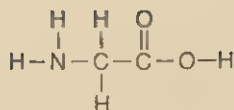
Figure 2.16 Generalized structure of an amino acid. Note the relative positions of the carboxyl (COOH) and amino (NH₂) groups.

their solubility in fat solvents. Steroids are very important molecules in the bodies of complex animals, where they are found primarily in the heart, blood vessels, and liver. In addition, certain vitamins and hormones which are produced in animal bodies are steroids.

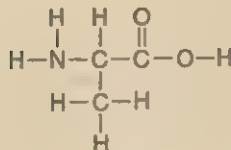
Proteins Many biologists regard proteins as being the fundamental compounds of living systems. Whether or not any one type of molecule may be singled out as "fundamental" is open to question, but proteins play many extremely important roles. Although they are structurally and functionally diverse, they exhibit certain characteristics which enable us to make some generalizations about them.

In terms of elementary chemical composition, proteins always contain carbon, hydrogen, oxygen, and nitrogen, and they usually contain sulfur as well. The micromolecular units are called *amino acids*, and a given protein molecule may consist of several hundred or even thousands of these units.* The structure of a typical amino acid is shown in Figure 2.16, where R represents a chemical group which is specific for a particular amino acid. The feature shared by

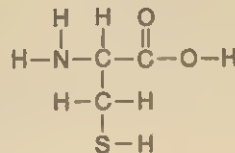
*Of the many amino acids known to chemistry, only twenty are commonly found in proteins. In referring to the total number of amino acids, we shall mean those twenty.



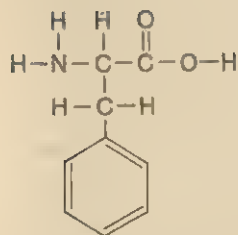
Glycine



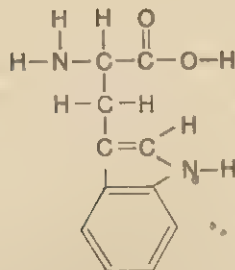
Alanine



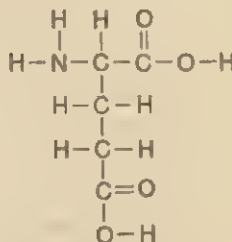
Cysteine



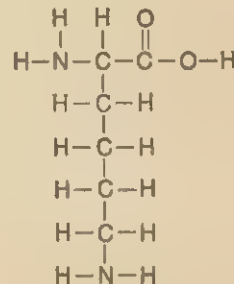
Phenylalanine



Tryptophan



Glutamic acid



Lysine

Figure 2.17 Structural formulas of several representative amino acids.

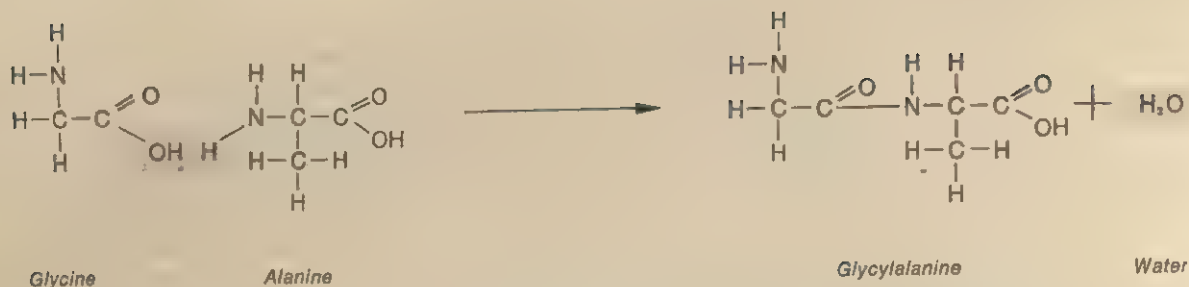


Figure 2.18 The combination of glycine and alanine by dehydration. Note the peptide bond formed between these two molecules by the splitting off of water.

all amino acids is a carbon atom (called the alpha carbon) to which is attached a carboxyl (COOH) group and an amino (NH₂) group. These compounds are called amino acids because of the amino and carboxyl (acid) groups. Figure 2.17 illustrates some of the diversity exhibited by the amino acids. A complete listing and illustration of their structure may be found in most textbooks concerned with organic chemistry.

When amino acids link together, they do so in such a way that the acid (COOH) group of one is attached to the amino (NH₂) group of another. The bond thus formed between the carbon of the acid group and the nitrogen group is termed a peptide bond. This can be illustrated by showing how two amino acids are joined together (Figure 2.18). In this particular example, the two simplest amino acids, glycine and alanine, are subjected to dehydration (water removal). As shown, the carboxyl group of one molecule gives up its OH and the amino group of the other reacting molecule gives up one H. Water is thus formed, and the two molecules are linked from carbon to nitrogen. By addition of any one of the twenty amino acids to this dipeptide, a tripeptide would be formed. In similar fashion, continued addition to the chain would lead to the formation of a large polypeptide chain, or large protein molecule. The specific amino acid sequence of any given protein molecule is called its *primary structure*.

When we consider that there are twenty different amino acids which may be arranged in any order to form a sequence of hundreds (and in the largest protein molecules, thousands) of amino acids in the formation of a single protein molecule, it becomes apparent that a vast number of different protein molecules can exist. This situation is analogous to having an alphabet of twenty letters with which to form words. If there is no prescribed sequence in which the letters must appear, then the number of words that can be formed becomes



almost infinite. As we shall see, this high degree of structural diversity is very important in the many and varied functional roles fulfilled by proteins in living systems.

Physical studies have shown that few proteins exist as a straight-chain sequence of amino acids. For the most part, they are not elongated molecules; rather, they are coiled or twisted in a number of ways, the most common of which is a spiral twisting called an *alpha helix*. The geometry of an alpha helix can be visualized by letting a pipe cleaner of certain length represent a straight chain of amino acids. If the pipe cleaner is coiled around a pencil by proceeding from the tip of the pencil to the eraser in clockwise fashion, an alpha helix is formed. Its shape can be seen more clearly if the pencil is then slipped out (Figure 2.19). Experimental evidence indicates that this alpha helix is produced from a straight chain molecule whenever weak hydrogen bonds pull adjacent parts of the molecule into a helical form.

Hydrogen bonding is thought to be an electrostatic attraction between the positively charged hydrogen end of a polar molecule and an unshared electron pair of one atom of another molecule. This situation is quite common in a chain of amino acids. The N—H structure of the peptide linkage presents a polar situation, while the C=O structure of the peptide linkage presents a pair of unshared electrons. Thus, a hydrogen bond is formed between the N—H group of a peptide linkage at one point in the chain and the C=O group of a peptide linkage in an adjacent part of the chain. Hydrogen bonding is an extremely important mechanism in protein structure according to the present concept. Apparently, it is responsible for the formation of the alpha helix, which constitutes the *secondary structure* of a protein molecule.

The protein molecule owes its ultimate configuration to the diversity of exposed chemical (R) groups comprising the amino acids which determine the primary structure of the molecule. Some of this diversity is illustrated in Figure 2.17, where the R groups may represent ring structures, acid groups, amino groups, or sulfhydryl (SH) groups. This diversity makes it possible for a number of bonding situations (including the hydrogen bond) to develop between adjacent groups. These interactions cause the molecule to fold upon itself still further, producing what is termed the *tertiary structure* of the molecule. This tertiary structure gives the molecule a final and specific surface configuration, leaving certain active groups exposed

Figure 2.19 An alpha helix configuration. Notice that the coils of the helix are clockwise. Protein molecules apparently assume this configuration after their synthesis from amino acids.

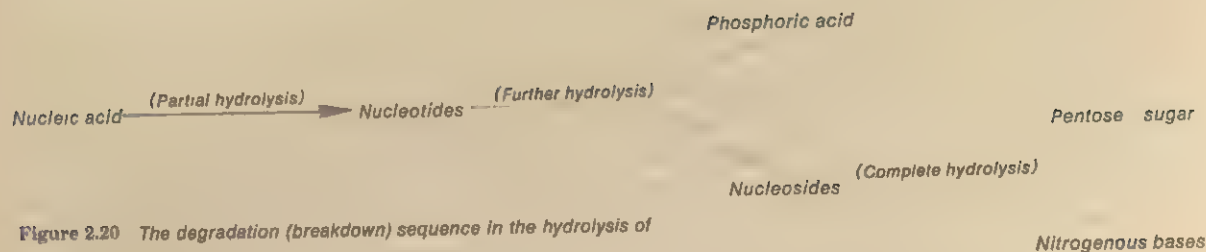


Figure 2.20 The degradation (breakdown) sequence in the hydrolysis of nucleic acids.

to react with other molecules, and also shielding certain groups from reaction with other molecules.

Although most of the active proteins within living systems exhibit the type of structure we have discussed, they may also assume a second type of configuration. Known as the *beta configuration*, it involves interaction or bonding between two or more polypeptide chains adjacent to each other. The secondary structure and tertiary structure which are characteristic of the protein molecules we have discussed does not occur in those with a beta configuration. Instead, the molecules remain long and fibrous, and are therefore sometimes called *fibrous proteins*. Biochemically, these proteins are generally far less active than the other type, which tend to be spherical or globular in form; rather, they function to a great degree as structural proteins in living systems. For example, they are the principal components of muscle, bone, and cartilage in the bodies of complex animals.

Earlier, we discussed enzymes and the role they play as organic catalysts in living systems. You will recall that we defined them as proteins. In the light of our discussion above regarding the structure of protein molecules, perhaps we are now in a better position to understand the specificity of enzymes as well as certain other aspects of their activity.

Enzymes belong to the group of globular or spherical proteins mentioned above, and each type of enzyme molecule has a very specific surface configuration due to its primary, secondary, and tertiary structure. The specific surface configuration leaves certain chemical groups exposed which will react quite readily with certain other chemical groups upon contact. Thus, it is not difficult to understand that an almost infinite number of different and quite specific enzymes having certain active sites (exposed chemical groups) may exist. Perhaps our previous analogy of a lock and key type of relationship between an enzyme and substrate molecule is now clearer and more meaningful.

Nucleic acids Although the nucleic acids have been known to

chemistry since the nineteenth century, their importance to living systems was not appreciated until recently. Of the four basic molecules of life that we have mentioned, there is more research at the present time in the nucleic acids than in any of the others. In fact, one of the nucleic acids, deoxyribonucleic acid (DNA) is sometimes called "the basic molecule of life." The role of the nucleic acids as the genetic material which directs and controls the metabolism of living systems will be discussed in a later chapter. Our aim at present is that of gaining some insight into the structure of these large organic molecules. Such insight is essential to an understanding of their functional roles in living systems.

The nucleic acids are threadlike macromolecules composed of thousands of atoms. There are two different types of nucleic acids, *deoxyribonucleic acid* (DNA), and *ribonucleic acid* (RNA). The difference between the two will become apparent as we consider the micromolecular units which make up these large macromolecules.

By treating DNA or RNA with mild acids, it is possible to hydrolyze them into smaller units called *nucleotides*. The nucleotides may be considered the micromolecular building blocks of the large macromolecular nucleic acids. However, the nucleotides themselves are relatively large molecules, and when they are hydrolyzed further with stronger acids, they break down into *nucleosides* and *phosphoric acid*. The nucleosides, under treatment with still stronger acids, break down into *pentose sugars* and *nitrogen-rich bases*. This sequence of events is illustrated in Figure 2.20. Thus, a nucleotide is

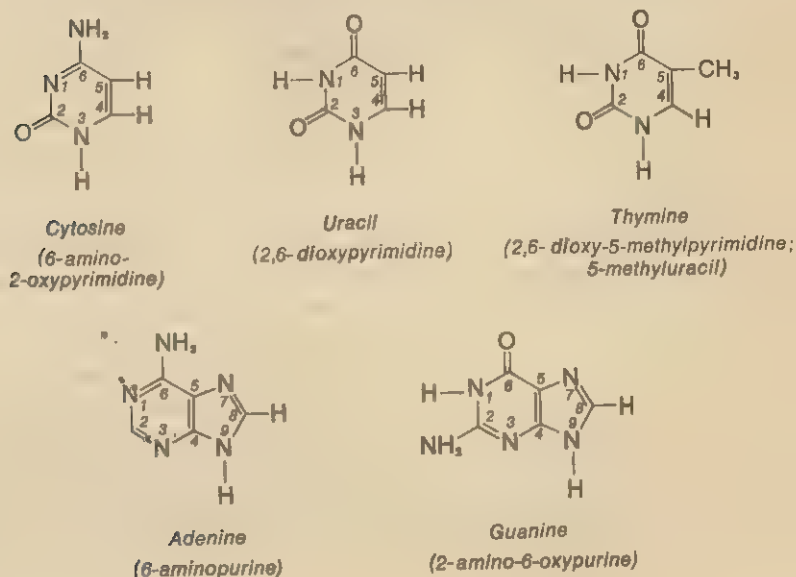
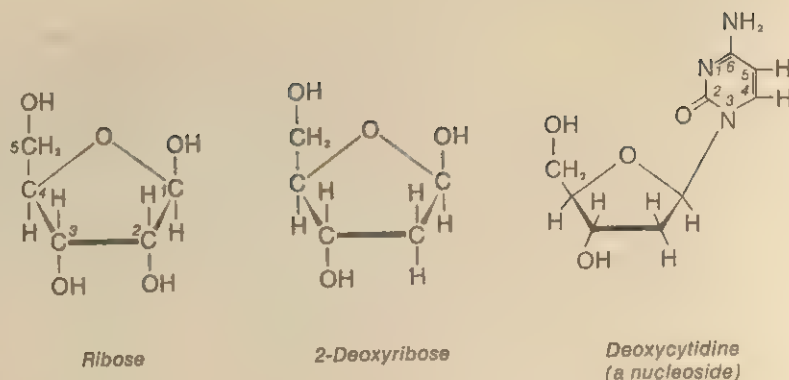


Figure 2.21 Structural formulas of the five nitrogenous bases found in nucleic acids. The upper three are pyrimidines, and the lower two are purines

Figure 2.22 Structural formulas of ribose, deoxyribose, and a nucleoside. This particular nucleoside consists of deoxyribose and cytosine bonded together.

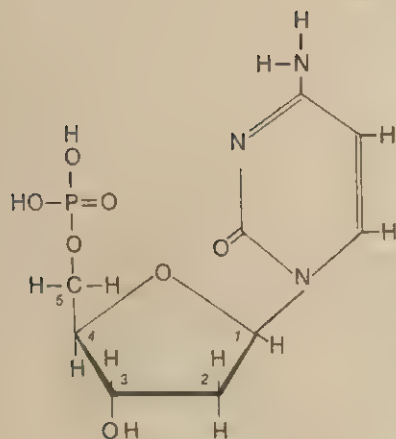


composed of a molecule of phosphoric acid, one of a pentose sugar, and one of a nitrogenous base. There are five major nitrogenous bases involved, and these fall into two categories, the *pyrimidines* and the *purines*. Three of the five (*cytosine*, *uracil*, and *thymine*) are pyrimidines and the other two (*adenine* and *guanine*) are purines. Although it is not essential at this point that we distinguish between pyrimidines and purines from a technical standpoint, it will be helpful to look at the formula of each base (Figure 2.21). As you can see, the three pyrimidines are single rings, and the two purines are double-ringed molecules.

The two basic types of nucleic acid, DNA and RNA, differ in the kinds of pyrimidine bases which compose them. The nucleotides of DNA contain cytosine and thymine, while those of RNA contain cytosine and uracil. Both contain the purine bases adenine and guanine.

The two pentose sugars found in nucleic acids are *ribose* and *deoxyribose*. You will recall that we gave the formula for ribose when we discussed carbohydrates (Figure 2.12) and we mentioned its importance in the nucleic acid molecule at that point. The ring structure for ribose and deoxyribose along with the structure of a nucleoside (nitrogenous base and ribose bonded together) are shown in Figure 2.22. The difference between the structure of ribose and that of deoxyribose is the absence of oxygen at position 2 in the deoxyribose molecule. The absence of an oxygen is implied in the prefix *deoxy-*, which means "take away an oxygen." The pentose sugar found in RNA is ribose, while that found in DNA is deoxyribose. This difference and the substitution of uracil for thymine in RNA constitute the primary structural differences between DNA and RNA.

A nucleotide is formed by adding phosphoric acid to a nucleoside, as shown in Figure 2.23. By this means, a nucleotide may be



Deoxycytidine-3-monophosphate
(a nucleotide)

Figure 2.23 Structural formula of a nucleotide. Compare with Figure 2.22.

formed involving any of the nucleosides (that is, a given nitrogenous base bonded to either ribose or deoxyribose).

As we have mentioned, DNA and RNA molecules consist of chains of nucleotides linked together, as shown in Figure 2.24a. As illustrated, the nucleotides are linked together by a phosphate group between position 5 of the ribose of one nucleotide and position 3 of the ribose of another nucleotide. Thus nucleic acid molecules exist as long chains of nucleotides, possessing a sugar-phosphate "backbone" from which various bases extend. This is represented diagrammatically in Figure 2.24b.

It is important to note that the linkage of nucleotides by phosphate groups is of a nonspecific type as regards the different nitrogenous bases. The specific bases in each nucleotide are not directly involved in the linkage. Therefore, the bases may occur in a variety of sequences, forming chains of varying lengths. This structural feature

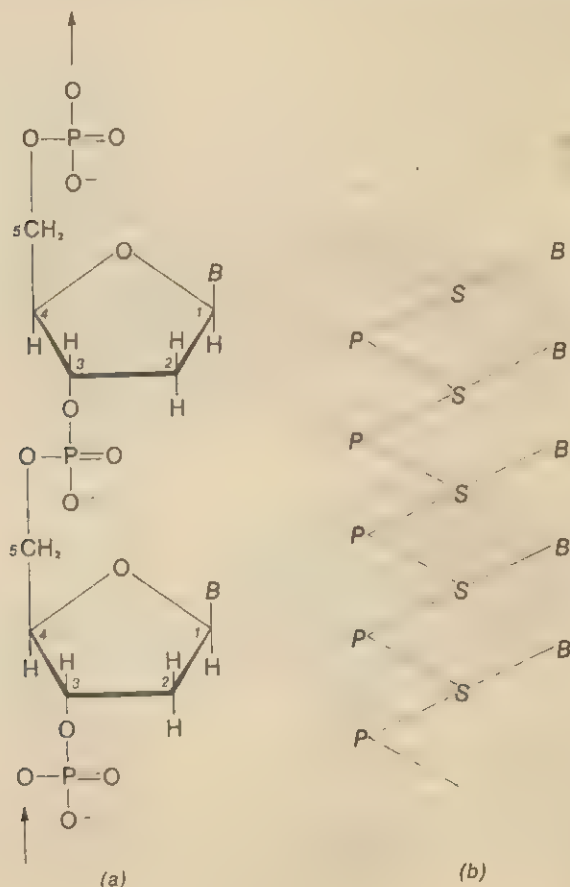
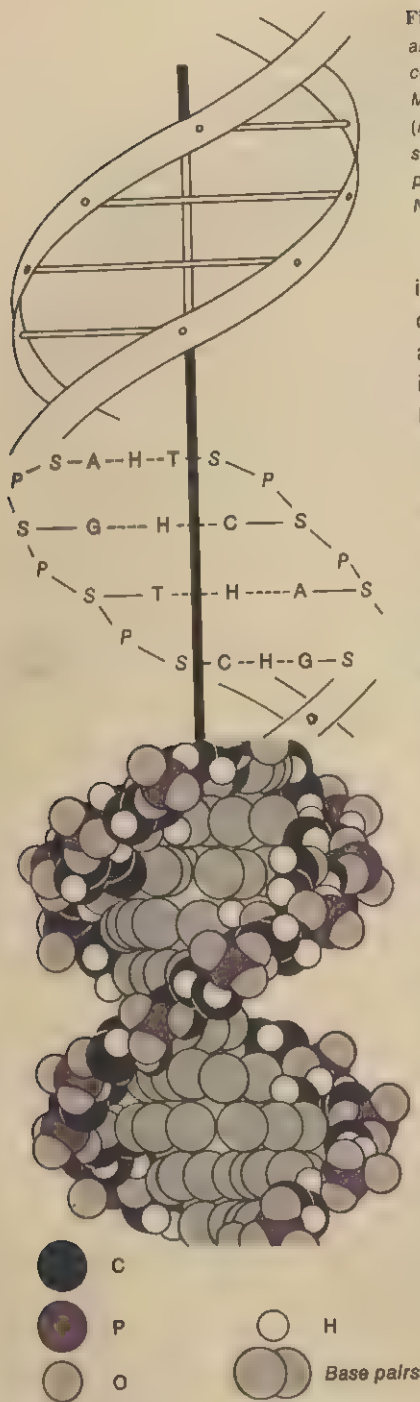


Figure 2.24 (a) Nucleotide linkage in the formation of a nucleic acid molecule. Is this DNA or RNA? What compounds might be attached at B? (b) Diagrammatic representation of the relationship among the sugar, phosphate, and base (purine or pyrimidine) molecules comprising a nucleic acid.

Figure 2.25 The helix of DNA, with three different ways of representing the molecular arrangement. Top, general picture of the double helix, with the phosphate-sugar combinations making up the outside spirals. The cross bars represent base pairs. Middle, a somewhat more detailed representation: phosphate (P), sugar (S), adenine (A), thymine (T), guanine (G), cytosine (C), and hydrogen (H). Bottom, detailed structure showing how the space is filled with atoms: carbon (C), oxygen (O), hydrogen (H), phosphorus (P), and the base pairs. [After C. P. Swanson, *The Cell* (Englewood Cliffs, N. J.: Prentice-Hall, Inc., 1964).]



imparts a great deal of variety to the nucleic acid molecule. When we consider that thousands of nucleotides may be present in the nucleic acid molecule in any sequence, it becomes apparent that an almost infinite variety of molecular types might exist. It will be shown in a later chapter that this structural feature of the nucleic acids is directly related to their physiological role in living systems.

For a number of years after most of the details regarding nucleic acids which we have discussed were known, the precise structure of the nucleic acid molecule was still a matter of almost pure speculation. However, in 1953 M. H. F. Wilkins, J. D. Watson, and F. H. C. Crick proposed a model for the structure of the DNA molecule based on information from X-ray diffraction and electron microscope studies. They surmised that the nucleotides composing a DNA molecule do not exist as straight chains, but that each nucleotide has about a 36-degree turn in its structure, causing the chain to coil into an alpha helix. Thus, a length of ten nucleotides make a complete 360-degree turn. They also determined that the diameter across the molecule is consistently about 20 Å* throughout the length of the molecule and that the molecule is therefore not a single chain or helix, but a double helix, with the two chains being coiled together like the coils in a rope. The two coils are held together by hydrogen bonds, which link the bases together across the double helix (Figure 2.25). Let us imagine a long, flexible ladder which is twisted from either end until a 360-degree turn is exhibited for every ten rungs. In this analogy, the sides of the ladder represent sugar-phosphate linkages, and the rungs represent the hydrogen-bonded base pairs. This is the concept of the DNA molecule which is generally accepted in biochemistry and biology, and it is frequently termed the *Watson-Crick model*.

It was further determined by physical and chemical analysis that there is a precise or specific quality in the bonding across the double

*Below the level of the millimeter there are three units of linear measurement that should be defined at this point. A millimeter (mm) equals 1,000 microns (μ); a micron equals 1,000 millimicrons ($m\mu$), and a millimicron equals 10 angstroms (Å). Therefore, $1\text{Å} = 0.1\text{ }m\mu = 0.0001\text{ }\mu = 0.0000001\text{ mm}$.

helix, that is, that certain bases must pair off with certain other bases. The diameter of 20 Å across the helix suggested that a pyrimidine must bond with a purine. You will recall that a purine molecule involves a double ring, and as a consequence, it is of greater diameter than a pyrimidine molecule. A distance of 20 Å would not accommodate two purines, according to size estimates, and it appeared to be too great a distance for a pair of pyrimidines. However, it was estimated that a purine bonded to a pyrimidine ought to fit the space very nicely. Upon hydrolyzing any given type of DNA completely, the relative proportions of the four nitrogenous bases may be determined. When this is done, the following relationships are evident.*

Adenine (A) = thymine (T)

Guanine (G) = cytosine (C)

$A \neq G$

$T \neq C$

$A + G = T + C$

$A + T \neq G + C$

It is evident from these relationships that adenine must be bonded to thymine and cytosine must be bonded to guanine across the double helix. In other words, for every adenine in a DNA molecule there must be a thymine, and for every cytosine there must be a guanine. It is extremely important to note at this point, however, that this characteristic of the DNA molecule does not affect the variability which can exist among DNA molecules with regard to the vast array of sequence of nucleotides which may exist in the chain in an "up and down" direction. It should also be pointed out that there are a few cases in which DNA apparently exists as a single strand rather than as a double helix.

The Watson-Crick model has withstood the rigors of numerous experimental tests since 1953. It has emerged as the best working model available for the structure of DNA. In fact, Watson, Crick, and Wilkins were awarded the Nobel prize in physiology and medicine in 1962 for their formulation of this model.

The precise structure of RNA is much less clear than that of DNA. In some cases it appears to be single-stranded, in others double-stranded, and in still others a combination of both. Its structural variability probably relates to its functional variability, which we will discuss in a later chapter.

* By substituting numerical values (for example, let A = 15 percent, G = 35 percent), these relationships may be made clearer.

2.6 In order to study biology on the molecular level, it is necessary to clarify certain fundamental aspects of matter and energy. Matter is defined as anything which occupies space and possesses mass, and it consists of fundamental units called atoms. Interactions of atoms produce ionic complexes, molecules, and compounds. Energy may be defined as the capacity to do work, and it is further characterized by the limitations implied in the first and second laws of thermodynamics. Matter and energy are closely interrelated in reactions involving atoms, molecules, or compounds.

Summary

The basic molecules of living systems are classified as carbohydrates, lipids, proteins, and nucleic acids. Each of these types may be distinguished from the others according to chemical composition and structural characteristics. In general, carbohydrates and lipids are composed of relatively simple molecules, while those of proteins and nucleic acids are extremely complex. Molecular structure in the proteins and nucleic acids especially can be correlated with their functions in living systems, where they play highly specific roles.

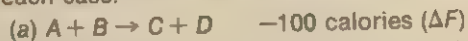
Questions

1 Define the following terms: atomic number, mass number, atomic weight, isotope, organic compound, nucleotide, pH, entropy, hydrolysis, alpha helix.

2 Explain why sodium and chlorine interact in a 1:1 ratio, whereas calcium and chlorine interact in a 1:2 ratio.

3 Sulfuric acid (H_2SO_4) dissociates in solution into $2\text{H}^+ + \text{SO}_4^{2-}$. The H_2SO_4 molecule therefore includes both ionic and covalent bonding. Diagram this molecule to show all electron relationships within it.

4 Which of the following reactions would you expect to occur spontaneously after the reactants are activated? Justify your answer in each case.



5 A certain solution has a pH of 9. Is it acidic or basic? How many grams of hydrogen ion would have to be added to or taken from a liter of this solution in order for the $[\text{H}^+]$ to equal that of a liter of water?

6 Define a buffer. Why are buffering systems highly important in living systems? See if you can find an example of a buffering system other than that used as an example in this chapter.

7 In what way or ways is carbon a rather unique element with respect to its role in living systems?

8 What is the Watson-Crick model and why might it be called a conceptual scheme?

9 The point is sometimes made that evolution of organisms from relatively simple to relatively complex forms could not possibly have occurred because this would be a violation of the second law of thermodynamics. Perhaps you do not feel qualified at this point to discuss the concept of evolution, but in terms of energetics, do systems *always* go toward increased entropy? Is the development of an animal embryo a violation of the second law? Incidentally, does a "law" of nature (such as the second law) *prescribe* or *describe* what happens in situations to which it applies?

10 We have observed that molecules of carbohydrates and fats are relatively simple, whereas those of proteins and nucleic acids are relatively complex. In living systems, the functions of carbohydrates and fats are relatively few and general (for example, glucose serves almost universally as a fuel substance), whereas the functions of proteins and nucleic acids are diverse and rather highly specialized. Attempt a correlation of molecular complexity and function based on the information in this chapter.

References *Baker, J. J. W., and G. E. Allen* *Matter, Energy, and Life*. Reading, Mass.: Addison-Wesley Publishing Co., Inc. 1965. Written especially to provide a background in physics and chemistry for students of biology, this book presents difficult material in a simplified form without distorting it.

Gamow, G. *Matter, Earth and Sky* (2nd ed.). Englewood Cliffs, N.J.: Prentice-Hall, Inc., 1965. A textbook of physical science enlarging upon many of the topics we have treated briefly in this chapter.

White, E. H. *Chemical Background for the Biological Sciences*. Englewood Cliffs, N.J.: Prentice-Hall, Inc., 1964. This is one of twelve brief textbooks making up a series entitled Foundations of Modern Biology. We shall cite each of these excellent books at one point or another, and some will be suggested in connection with more than one chapter. White's book will prove to be very helpful in understanding the concepts we have introduced in this chapter.

 In addition to the three references listed, any modern textbook of chemistry or physics contains sections which are relevant to this chapter.

3

The

organization

of living

systems

3.1 The nature of life

All matter is composed of atoms and molecules, but a great difference in degree of complexity exists between matter not associated with living systems and that which is so organized as to exhibit the phenomenon we call life. This should be apparent from our previous consideration of the macromolecules characteristic of living systems. Of course, some molecules found in living systems are relatively simple, but the very existence of such macromolecules as proteins and nucleic acids in these systems is an indication that such systems are highly complex.

Both small and large molecules, ionic compounds, and complex aggregations of chemical substances are associated within living systems in such a way that various phenomena are manifested which are foreign to the nonliving world. In this chapter, we shall attempt to gain some degree of understanding with regard to the nature and organization of this "living" matter as it is exhibited by the great variety of organisms found on earth.

It is a matter of some concern to the biologist that he cannot define in precise terms that which he studies and tries to understand. The term life is extremely difficult to define in exact terms because it is something of an abstraction. We find it necessary, in dealing with other abstractions, to define them in terms of their characteristics. The word "beauty" is such a term. Beauty is known by any number of concrete and easily defineable characteristics, but it is not subject to definition according to material concepts. Even such a down-to-earth term as "fire" comes under this classification. We know it by its characteristics. It is hot, it burns, it destroys, it is the *result* of materially defineable phenomena, but it escapes exact definition itself.

Thus it is with the term life. At extremes in the continuum of organization of energy and matter, we can easily recognize the difference between a living organism (for example, a horse) and a nonliving object such as a rock. However, as we proceed from the extremes of this continuum toward the middle, our problem becomes more complex. In fact, it is controversial as to where the line should be drawn in the continuum of structural organization and chemical activity. However, we must realize that what we call life is the result of a specific organization and activity of chemical substances. When this level of organization and chemical activity is irreversibly destroyed, life is destroyed, and death results. Thus, the term life is probably best considered an abstraction or a literary term, not a scientific one.

Nevertheless, we can go far toward understanding life by studying its characteristics. We know by observation and experimentation that living systems are capable of carrying on elaborate chemical activities (metabolism); they grow, they reproduce themselves, they ex-

hibit responsiveness to stimuli, and they adapt to environmental circumstances. These five characteristics are considered to be sufficiently important to have a chapter devoted to each of them.

A useful and somewhat more precise concept of life may be gained through an application of the second law of thermodynamics to living systems. As we pointed out in Chapter 2, the second law predicts that when a system is "closed," or left to itself, it will proceed toward a state of disorganization. In other words, there will be an increase in entropy and a decrease in enthalpy. A situation in which low enthalpy and high entropy prevail represents stability, and all systems left to themselves proceed toward greater stability or equilibrium. Since a living system represents a highly organized (nonrandomized) state of energy and matter, it would seem to contradict or "disobey" this law. However, the second law of thermodynamics does not preclude niches or pockets of organization in the physical world (provided free energy is supplied to the system). Evidently, this is the situation in a living system. It maintains high enthalpy and low entropy as a result of having access to a constant source of free energy, and in fact, it is able to extend its degree of organization. When the source of free energy is removed, the living system proceeds (in accordance with the second law) to a state of thermodynamic equilibrium. We call this equilibrium death.

In a sense, then, life might be defined as a fight against thermodynamic equilibrium. No individual living system (whether it be a cell or an organism) ever "wins" this fight, but it may pass its "weapons" on to a subsequent system through reproduction. In other words, when we view life in terms of energetics, it is a *state of organization* capable of utilizing free energy. Through various transformations of this energy, it keeps itself organized. In the process of doing so, it carries out the various activities that we referred to as characteristics of life. The matter found in living systems is simply a special case of physical matter, and we may reasonably assume that its unique characteristics are a reflection of its highly organized and self-perpetuating state of existence. To say the very least, living systems constitute no exception to the second law of thermodynamics, nor to any other basic principle of chemistry or physics.

- 3.2 The physical material that constitutes living systems is called *protoplasm* (Gr. *protos*, first + *plasma*, form). It is typically a more or less viscous, translucent kind of material that is a complex mixture of many substances, although there are variations in its physical and chemical composition. It may contain material which is not, within itself, a necessary accompaniment of life, such as fat or starch

particles. Whenever the term protoplasm is used, however, it refers to a given quantity of matter in which the characteristics of life are manifested. By means of special chemical techniques, much has been learned about the nature and organization of this material. Such knowledge has shed considerable light on certain fundamental life processes. Furthermore, many important problems which are the concern of modern biology involve the physics and chemistry of protoplasm.

Chemical composition of protoplasm From the chemical standpoint, it might logically be supposed that protoplasm should contain rare or unusual elements which are completely absent from nonliving matter. This is not the case. The most abundant elements found in protoplasm are also among the most abundant in the nonliving world. The major elements found in most protoplasmic systems, and their approximate relative percentages by weight, are shown in Table 3.1. In addition to those elements listed, traces of other elements (for

Table 3.1 The elements most commonly found in living systems*

Name	Symbol	Weight percentage
Bulk elements		
Oxygen	O	65
Carbon	C	18
Hydrogen	H	10
Nitrogen	N	3
Calcium	Ca	2
Phosphorus	P	1
Total		99
Lesser elements		
Potassium	K	—
Sulfur	S	—
Sodium	Na	—
Chlorine	Cl	—
Magnesium	Mg	—
Iron	Fe	—
Copper	Cu	—
Manganese	Mn	—
Cobalt	Co	—
Zinc	Zn	—
Total		Less than 1

*Approximate relative abundance

Table 3.2 *Constituents of protoplasm*

Substance	Percentage
Water	75-90
Electrolytes and other inorganic compounds	1- 1.5
Proteins and nucleic acids	7- 10
Lipids	1- 2
Carbohydrates	1- 1.5
Other organic compounds	Less than 1

example, iodine and boron) are usually present. These trace elements are highly variable quantitatively in different protoplasmic systems. They constitute only a small fraction of 1 percent of the total matter in any given living system.

The elements found in protoplasm do not actually exist in elemental form, although some of them are present as ions. In this form, they are functional in such processes as energy transfer, enzymatic activity, nerve conduction, and membrane permeability. For the most part, elements are organized into compounds, both organic and inorganic. Hence, there is a range in complexity of organization all the way from ions to the large macromolecules which we discussed in the preceding chapter.

The inorganic compounds of protoplasm are water and a variety of electrolytes (acids, bases, and salts). The organic compounds include carbohydrates, lipids, proteins and nucleic acids. The average relative amounts of these substances in protoplasmic systems are as shown in Table 3.2.

It should be pointed out that 'average' or 'typical' protoplasm does not exist, since protoplasmic systems vary so widely. However, the approximations listed above give us some idea of the relative abundance of these substances in protoplasmic systems and may generally be considered typical.

The physical nature of protoplasm. From the foregoing discussion it might be inferred that the most outstanding feature of protoplasm is its chemical make-up. Although it is true that some highly unique materials such as enzymes and nucleic acids go far toward making this a valid assumption, there is another side to the story. The compounds and elements of protoplasm might be mixed together in the exact proportions found in a given unit of protoplasm, but the resulting material would not be alive. After a unit of protoplasm has died, it is no longer protoplasm by correct definition. The ingredients are still all present, but the organization is lacking. The

one factor that renders such a chemical mixture living, therefore, is the physical relationship which the various components bear to each other.

A protoplasmic system is a multiphasic system, that is, it consists of molecular aggregates and particles of various sizes all of which are contained in a liquid medium. Multiphasic systems may be classified on the basis of the size of the particles involved. If the particles are sufficiently small to form a homogeneous dispersion throughout the medium, they are said to be in *solution*. If their size is such that they settle out of the medium in response to gravity, they are said to be in *suspension*. Finally, if the particles in such a system are intermediate in size, that is, too large to go into solution and too small to settle out, they are said to be *colloidal*. The range in size of colloidal particles is 0.001 to 0.1 μ . Thus particles as small as 0.001 μ or smaller go into solution, while those as large as 0.1 μ or larger settle out. Particles of intermediate size are dispersed in the medium, forming a colloidal system.

A protoplasmic system is a combination of several substances in solution and several types of particles in suspension. The solvent, of course, is water, and it is also the liquid medium or phase in which colloidal particles are dispersed.

It is beyond the scope of our treatment here to discuss the various types of colloidal systems which may exist in protoplasm. It is sufficient for our purposes to understand that protoplasm is a colloidal system involving solids (for example, fibrous protein aggregations) and liquids (for example, oil or fat droplets) dispersed within a liquid. In such a system, many reactions occur at the surfaces of particles or aggregations rather than between individual molecules. Furthermore, the direction or rate of such reactions depends to a great degree upon the electrical charges at the surfaces of the highly polarized particles, as well as depending upon the size and shape of each of them.

Many of the characteristics of protoplasm, including the formation of large macromolecular complexes called *organelles*, may at least partially be explained on the basis of the characteristics of a colloidal system. However, it would probably be a mistake to assume that all properties of protoplasm can be duplicated by any test-tube colloidal complex.

Let us return to our earlier statement that physical relationships within protoplasmic systems are ultimately responsible for those characteristics which we summarize by the term living. Perhaps an analogy will clarify this point.

Suppose a master watchmaker invents a clock whose parts are so intricately arranged that only he knows the secret of its operation.

Suppose further that he dies, and the clock is given to a novice. Upon observing the clock and its parts, this second person might well conclude that the clock operates successfully because it is composed of certain wheels and gears. In a sense, of course, this is true. It could hardly operate without them. However, many things are composed of wheels and gears that do not keep time, and in the final analysis, it is the physical relationship which these parts bear to each other that makes the instrument a clock. If the novice tries to take it apart, he will have wheels and gears, but he will not have a clock and never will again unless he can learn the secret of the original relationships. There is yet another point to be made from this analogy. When the master craftsman originally made the clock, he put a great deal of his "genius" into it. Does this mean that there is some mysterious influence, undefinable in physical and chemical terms, still floating around inside the clock? Not at all. His genius is measurable by its results, and we understand that the word is used as a literary one.

Only within recent decades have biologists as a group come to view protoplasmic systems from this clock, or mechanistic approach.* The mechanistic point of view is a conceptual scheme within whose framework we have found it possible to launch other conceptual schemes, thus fulfilling the highest requirements of science.

Let us carry our analogy of the clock one step farther. Suppose the novice to whom the clock was given has great difficulty in taking it apart in order to observe its inner workings. In exasperation, he finally takes a sledge hammer and smashes the clock. Because of this drastic action, a random dispersal results. The task of the novice in understanding the inner structure of the clock is now complicated by the fact that it is greatly distorted. Although this may be straining an analogy, we are faced with something of the same difficulty in studying protoplasm. In getting at the contents of cells, drastic treatments are usually necessary to break them down to their component parts. Thus, when we make either a chemical or a physical analysis of protoplasm, we cannot get a very accurate picture of the actual relationships which exist in the functional or living state.

Because the machinery of protoplasmic systems is quite intricate, there are formidable barriers which stand in the way of understanding it very well, to say nothing of the immense task of putting it

* It should not be inferred from this analogy that the biologist who takes this view of the living cell is obliged to postulate a creator to correspond to the master craftsman. He may or he may not, depending upon his own personal philosophy. Should he believe that a supreme being originally set the balance of protoplasm, however, this would not make him any less a mechanist in terms of present-day biological processes. This problem is dealt with more fully in Chapter 12, and you may wish to read this passage at this point.

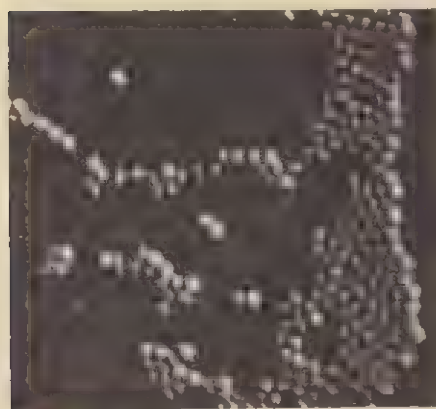
together synthetically. Hence, most biologists are not overly optimistic that either the goals of complete understanding or the artificial production of living protoplasm are near accomplishment, although great strides have been made toward both. *Thus far, life seems to come only from previous life in an unbroken chain, at least under conditions which prevail at present on earth.*

We can, however, come to some understanding in regard to a few of the physical principles governing the organization of protoplasm, although many which are known require for their understanding a knowledge of concepts and principles that are beyond the scope of this text. Some of those which are profitable to us will be introduced in later chapters.

3.3 The cellular level of organization Protoplasm is typically maintained in units called cells. As a unit, the cell is considered by most biologists to represent the level of organization in the continuum of matter and energy which constitutes the simplest living system. From a structural viewpoint, the cell constitutes a kind of building block for the more complex (multicellular) living systems. Although some organisms consist of only one complete unit of protoplasm, and hence are said to be unicellular, the great majority of organisms are made up of more than one protoplasmic unit and thus are multicellular.

Let us note at this point that the cell is the smallest and least complex unit of matter which can unquestionably be called living.* This means that, within limits of specialization, it can carry on all the basic activities which characterize organisms. In other words, the activities to which we refer as metabolism, growth, reproduction, responsiveness, and adaptation are, in the final analysis, carried on by protoplasm. It should be kept in mind as one considers these fundamental activities that a cell is a highly organized entity whose material substance is so ordered as to warrant its being considered "living." *In its own right*, therefore, and not simply by virtue of its association with other such units in a complex organism, the cell holds this unique distinction. More precisely, a cell is a system of

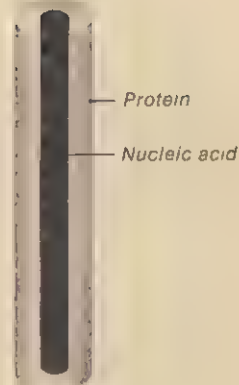
*Viruses, some of which are causative agents of diseases in various plants and animals, are extremely small units of matter which manifest certain characteristics associated with protoplasm. Typically, they consist of nucleic acid coated with protein (Figure 3.1). Although they reproduce themselves they do not carry on the complex chemical activities associated with protoplasm, and many biologists do not consider them to be living in the strict sense of the word. In fact, they can reproduce only within living cells. Certainly they are complex, on the molecular level, and perhaps they should be considered an exception to the strict distinction that is usually drawn between living and nonliving units of matter. In the final analysis, of course, the problem is largely one of definition.



(a)



(b)



(c)

Figure 3.1 Some representative viruses. (a) Electron photomicrograph of tomato bushy stunt virus, magnified 57,000 times. (b) Electron photomicrograph of tobacco mosaic virus, magnified 65,500 times. (c) Diagram of a virus, showing typical structure. A core of nucleic acid is surrounded by an "overcoat" of protein. (Electron photomicrographs courtesy of Dr. R. C. Williams.)

supramolecular complexes so organized as to take in free energy and matter. By so doing, it is able to maintain and extend its organization, and exhibit the properties listed above which emerge at this level of organization.

Cells show a great deal of variability in size, shape, structure, and function. This is especially true of the various cells making up a complex multicellular organism, where the association of cells in the formation of tissues is accompanied by a division of labor. Some of this diversity is shown in Figure 3.2. On the other hand, there are many structural and functional features which most cells have in common. Because of these common features, we permit ourselves to speak of a "typical," or "average," cell, although such a cell is quite mythical.

When viewed with an ordinary light microscope, the typical cell appears as a unit separated from its environment by a *plasma membrane* enclosing the protoplasm (which consists of a *nucleus* and *cytoplasm*). In plants, a rigid *cell wall*, composed chiefly of cellulose, typically surrounds the cell and delimits it as a unit from others. This wall is nonliving and is not strictly a part of the cell, having been formed by the cytoplasm during its inception and growth. The plasma membrane lies just within this wall. Most animal cells, in contrast, are simply limited by their plasma membranes, although

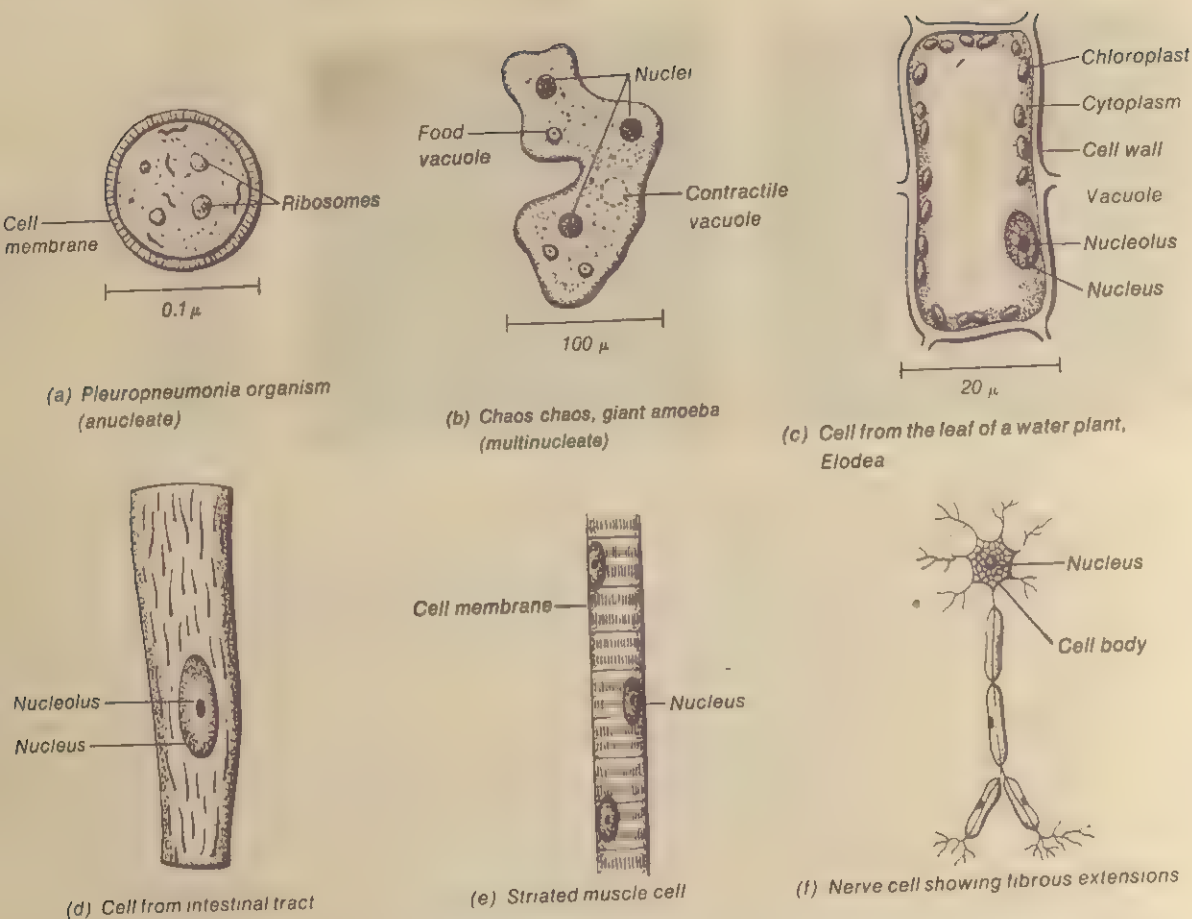


Figure 3.2 Various types of cells. Note the many differences in size, shape, and structure, especially in cells (a), (b), and (c). Cells (d), (e), and (f) are all from the body of a complex animal.

some possess a flexible, nonliving *pellicle* which corresponds to the plant cell wall.* Inside the cell, the nucleus appears to be separated from the cytoplasm by a *nuclear membrane*. It should be pointed out that in a few types of cells this definite nucleus-cytoplasm relationship does not exist. For example, the pleuropneumonia organism (Figure 3.2) has no organized nucleus as such; rather, nuclear materials are scattered throughout the cytoplasm. This organism is

* Since there is some confusion as to whether or not one includes the cell wall or pellicle when he speaks of a cell, the term *protoplast* is widely used to describe the entire unit lying within any such nonliving structure. Some biologists use the terms *protoplast* and *cell* synonymously.

approximately $100\text{ m}\mu$ ($1,000\text{ \AA}$) in diameter, and may represent the lowest organizational level of protoplasm that can be considered a living cell. At the other extreme, one of the largest cells known is that of the giant amoeba, *Chaos chaos* (Figure 3.2), which is approximately $100\text{ }\mu$ ($1,000,000\text{ \AA}$) in diameter and is multinuclear. But the typical nucleus-cytoplasm ratio is one nucleus per cell.

The protoplasm within the nucleus is called *nucleoplasm*, and it contains one or more dense bodies known as *nucleoli*, as well as a granular mass called the *chromatin network*, or simply chromatin material. When a cell enters into a divisional cycle, the chromatin assumes the form of discrete *chromosomes*. The number of chromosomes thus formed is usually constant for a given species of organisms. When viewed in the living condition with an ordinary light microscope cytoplasm appears as a somewhat homogenous, translucent material containing refractile bodies of different sizes. In many cells, the cytoplasm appears to be thicker or more viscous (*gel* state) around the periphery and less viscous (*sol* state) toward the center of the cell. Whenever such a distinction is made, the outer portion is called the *ectoplasm* and the inner portion is called the *endoplasm*. The sol-gel change which occurs as cytoplasm alternates between these two physical phases is a reflection of its colloidal nature. Although several bodies lie within the cytoplasm, most of them are difficult to see in the living cell with an ordinary light microscope. These bodies include *mitochondria*, a structure called the *Golgi complex*, and various granules, yolk bodies, and crystals. Under ideal conditions of observation, the *centrosphere* of the animal cell can be distinguished from the surrounding cytoplasm. Less difficult to see are the *plastids* found in the cytoplasm of many plant cells, of which the green *chloroplasts* are the most common.

In order to observe the more intricate structural details of cells, one must either use certain specialized types of microscopes, or else the cells must be killed and stained. Sophisticated microscopic techniques employ forms of radiation other than visible light, or else take advantage of special chemical and physical features of the different parts of the cell. Staining methods are based on the differential chemical nature of the various parts of the cell, which is reflected by their differential affinities for certain dyes. Figure 3.3 shows the various parts of "typical" plant and animal cells which can be observed by using a combination of microscopic and staining methods.

As is generally true in any area of science, our knowledge of living systems has advanced as techniques for studying them have been developed. An excellent example of this is the invention and development of the electron microscope (Figure 3.4), which became generally available in the early 1940's. By the use of this instrument,

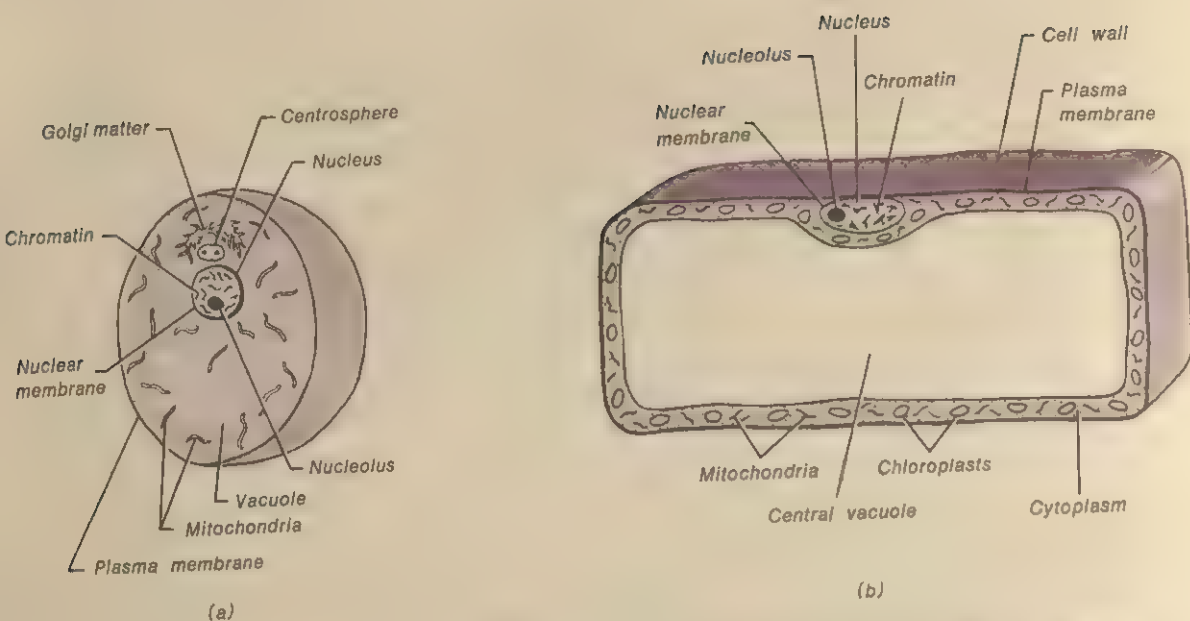


Figure 3.3 Representative cells in sectional view, magnified about 2,000 times
(a) Animal cell. (b) Plant cell.

extremely intricate details of cellular structure have been observed. Compared with the ordinary light microscope (which cannot be made to magnify over about 2,000 diameters with clarity), the electron microscope is a powerful instrument indeed. It magnifies at 200,000 diameters with clarity, and by using special photographic methods, even greater magnification may be obtained. The source of radiation in the electron microscope is a beam of electrons which is passed through magnetic fields and through the specimen to cast an image on a photographic plate. This image, or picture, can then be viewed by the human eye. There are some disadvantages inherent in the use of the electron microscope; not only is it an expensive and complicated instrument, but materials to be studied must be sliced ultrathin and dried thoroughly. Furthermore, since beams of electrons must travel through a vacuum, it is necessary that materials be prepared in such a way that they will not be distorted under these rigorous conditions. Needless to say, cells cannot be studied in a living state with the electron microscope; they must be killed, treated with chemicals, and sliced under the most exacting conditions.

Nevertheless, electron microscopy has yielded a wealth of information about cell structure which would not have been attainable otherwise. In Figure 3.5, for example, we see something of the de-

tailed structure of mitochondria, the nuclear membrane, and other inclusions which we have yet to discuss. Based on a number of observations with this powerful instrument, plus certain biochemical and biophysical data, we now conceive of the generalized or "typical" cell as shown in Figure 3.6.

In general, the structural entities (subcellular particles) in the cytoplasm of the cell can be classified as *cytoplasmic inclusions* or *cytoplasmic organelles*. The cytoplasmic inclusions are such structures as glycogen granules, fat droplets, and yolk bodies. Most of

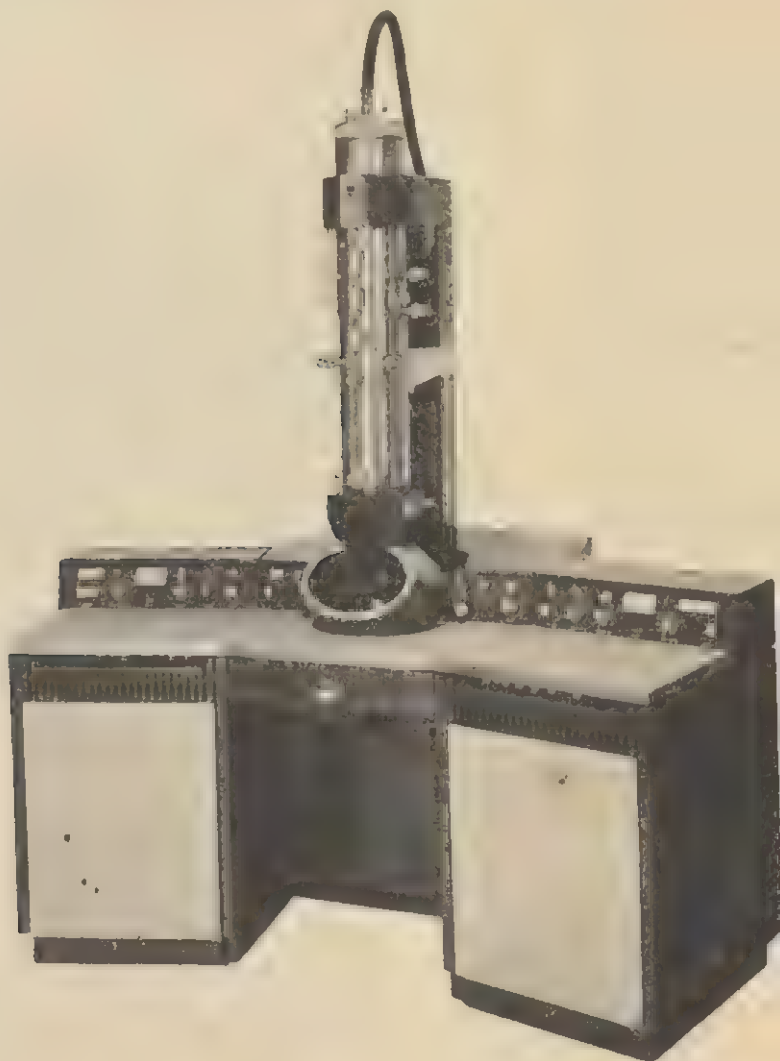
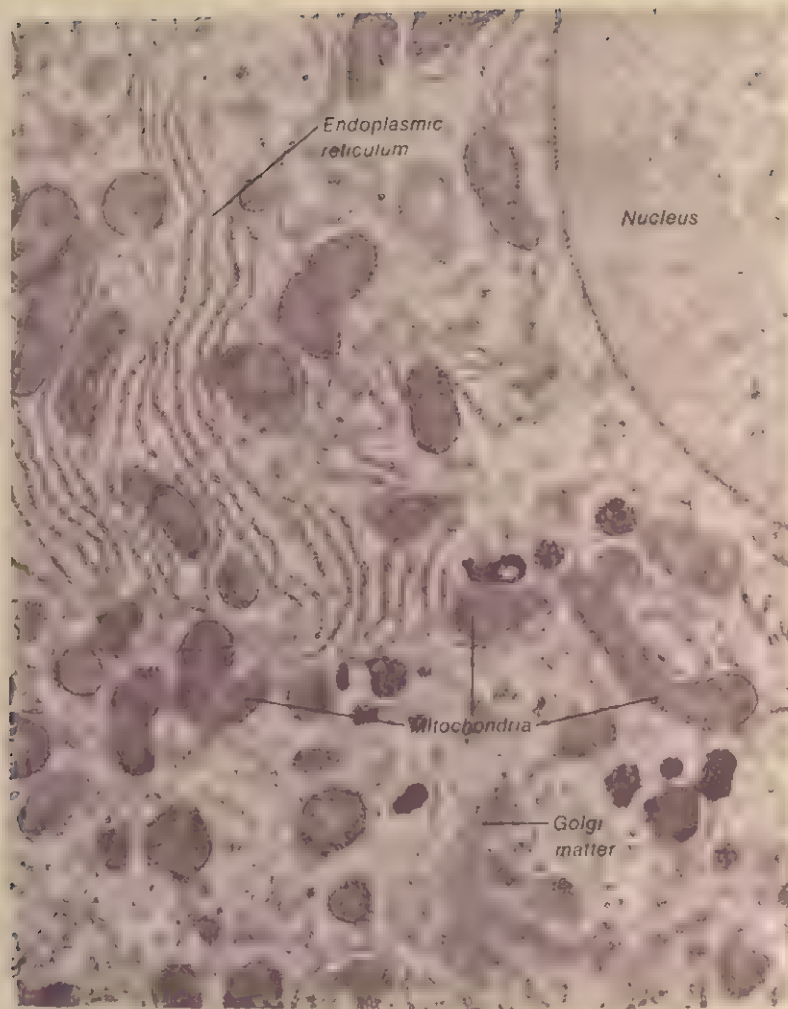


Figure 3.4 A modern electron microscope, the Norelco EM 300 (Philips Electronic Instruments.)

Figure 3.5 A portion of a rat liver cell in thin section, as photographed by the electron microscope and magnified about 50,000 times. Note the internal structure of the mitochondria. A portion of the endoplasmic reticulum is shown; note attached ribosomes, which appear as small dots. Several structures discussed in the text may be seen in this view of the cell. (Courtesy of Dr. K. R. Porter.)



these inclusions are rather passive entities which represent stored food materials in the cell. In contrast, cytoplasmic organelles are functional entities or sites of activity in the cell. Because of their importance to living systems, we shall list and discuss the more important organelles in turn.

The cell membrane The electron microscope shows the cell membrane (sometimes called the plasma membrane) to be a double-layered structure ranging from 65 to 100 Å in thickness. Chemical analysis has shown it to be composed of lipid and protein. The lipid components are compound lipids and are primarily the phospholipids lecithin and cephalin. The protein components belong to

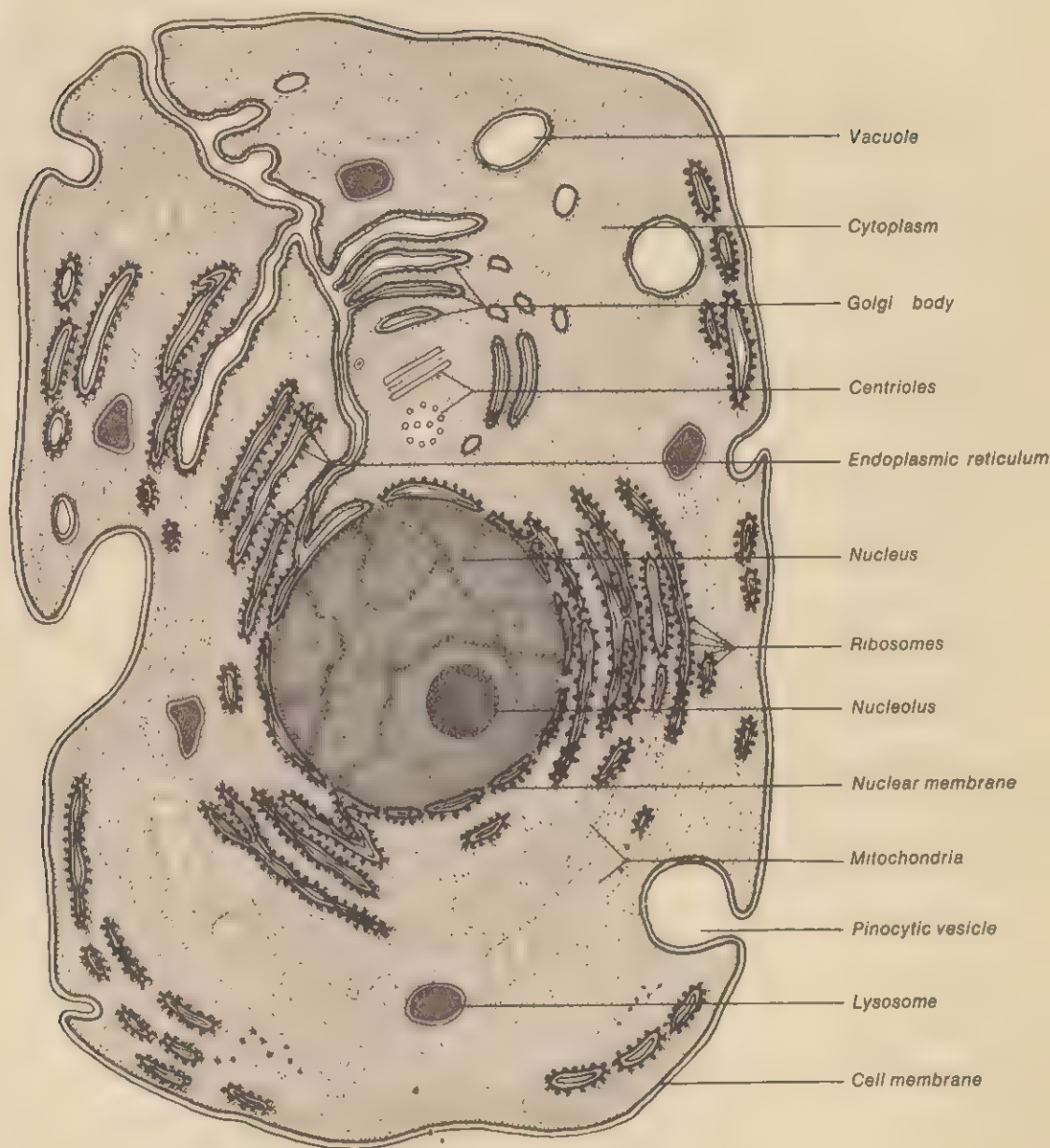


Figure 3.6 Highly diagrammatic representation of a generalized cell, showing parts discussed in the text. This figure is based upon many lines of evidence, especially electron-microscopic studies. The two-dimensional appearance represents a thin slice as it might be prepared for electron photomicrography.

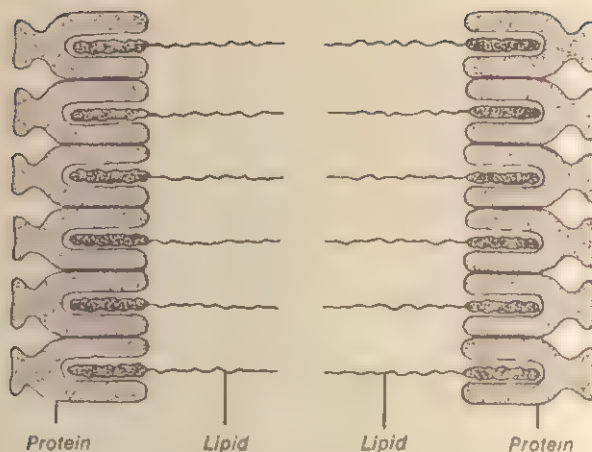


Figure 3.7 Theoretical model of the cell membrane in sectional view. Two layers of closely packed protein molecules enclose a double layer of less compact lipid molecules.

the fibrous protein group. A theoretical model of molecular arrangement in the cell membrane has been proposed by several investigators. According to this concept (Figure 3.7), the cell membrane is composed of a double layer of lipid molecules sandwiched between two layers of protein. This model is based on electron-microscope studies, X-ray-diffraction studies, chemical analysis, and known physiological properties of the membrane.

The cell membrane serves as a boundary between the external environment and the internal environment of the cell. It thus represents a barrier which all molecules must traverse in entering or leaving the cell. This includes the molecules supplying the energy that keeps the cell organized and functional, the micromolecules which constitute the building blocks of the basic macromolecules, and the various by-products or waste materials which result from the activities of the cell. Thus, the cell membrane is permeable, that is, it "permits" the passage of substances through it. To be more precise, it is *selectively* or *differentially* permeable, since some ions or molecules pass through it while others are prohibited from doing so. Therefore, in regard to permeability, it "selects" some substances and "rejects" others. The factors involved in cell membrane permeability will be discussed in Chapter 6.

Mitochondria The mitochondria are filamentous or granular organelles ranging in size from about 0.2 to 0.7 μ in diameter. Their size, shape, and distribution is relatively constant in cells of the same type; however, cells of different organisms or tissues show considerable variability in this regard. Figure 3.3 shows how the mitochondria are scattered throughout the cytoplasm of typical plant and animal cells.

Although mitochondria can be seen by using the ordinary light microscope, very little detailed structure is discernible by this method. However, the electron microscope reveals a very intricate and detailed structure (Figures 3.5, 3.6, and 3.8). The mitochondrial membrane, like the cell membrane, is a double structure composed of lipid and protein. The inner membrane is thrown into a series of folds forming "shelves" that extend into the matrix (liquid portion). These folds, or shelves, are known as *cristae*, and they take various forms in the mitochondria of different cell types. Figure 3.8 represents a somewhat generalized mitochondrion, and its structure may be considered representative.

Mitochondria play a very important role in living systems; the bulk of the chemical energy of fuel molecules which enter the cell is extracted and conserved within them. Because of this role, mitochondria are often called the "powerhouses" of the cell. We will have more to say about mitochondria in our discussion of metabolism (Chapter 6); for the present, it is sufficient that we recognize their important role in those energy transformations which make possible the continued organization and activity of the cells within which they are located.

The number, distribution, and structure of mitochondria relate directly to their function within living systems. They are very numerous in cells whose activities are associated with the expenditure of large amounts of energy (for example, muscle cells of the animal body). Furthermore, they are localized in particular regions of cells where energy expenditure is high; for example, they are highly concentrated in the contractile fibers of muscle cells and in regions adjacent to the cell membranes of nerve cells.

In terms of thermodynamics, mitochondria are more directly involved than any other organelles in the maintenance of the high enthalpy and low entropy characteristic of living systems. Since energy must be put into a system if it is to resist an increase in

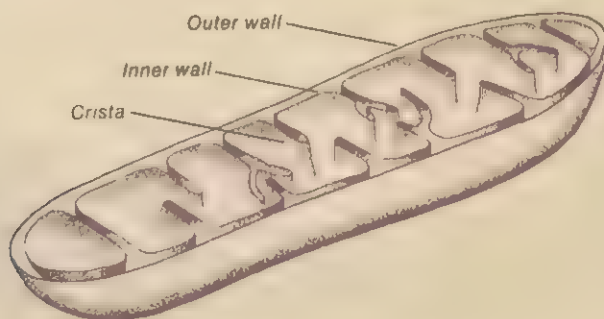


Figure 3.8. Cutaway view of a mitochondrion, drawn schematically. Note that the cristae form loosely connected compartments.

entropy, an efficient mechanism for translating this energy into a utilizable form is essential. It is to this particular role that mitochondria are adapted, and this is reflected in their structure, number, and distribution within the cell.

Plastids Plastids are found in at least some cells of virtually all members of the plant kingdom, except for certain of the least complex forms. They vary in size, number, shape, distribution, and chemical organization, as well as in color. On the basis of presence or absence of color, they may be classified into two major groups: the *leucoplasts* (colorless) and the *chromoplasts* (colored). This distinction is rather artificial, however, since it is known that leucoplasts may change into chromoplasts.

The most important and widespread of the plastids are the chloroplasts (Figure 3.9), which are found in all green plants. They are particularly abundant in cells actively engaged in the process of photosynthesis, which occurs only in the presence of the green pigment chlorophyll. The chloroplast owes its color to this pigment. Chloroplasts are typically ovoid in shape and are bounded by a double-layered membrane. Within this membrane is the matrix or *stroma*, and it contains granules called *grana*. Electron microscopy reveals that these grana consist of layers of membranes stacked on top of each other and joined together by a series of paired membranes which also extend into the stroma (Figure 3.10). It is within the layered membranes of the grana that the chlorophyll is localized, as well as certain enzymes which are functional in the photosynthetic process.

Chloroplasts, like mitochondria, are functional in the transformation of energy. The process of photosynthesis, through which the sun's energy is transformed into chemical energy, is a first step in the world of life toward reversing the trend to increasing entropy. Thus, the functional role of the chloroplast is vital not only to the life of the plant cell which contains it, but to living systems in general, since all organisms ultimately benefit from the energy of sunlight.

The endoplasmic reticulum, ribosomes, and microsomes The electron microscope has shown the cytoplasm to be traversed by a *reticulum* (network) of strands and vesicle-like bodies. This network

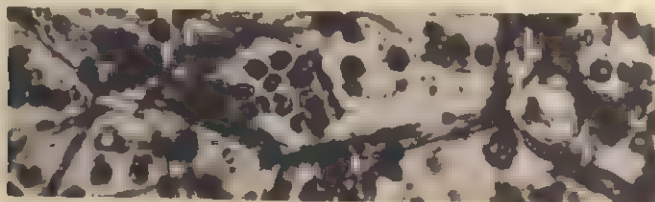
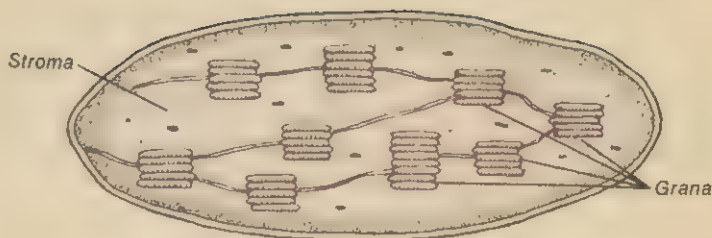


Figure 3.9 Microscopic view of leaf cells, showing several chloroplasts. They are particularly numerous in the small cell near the center of the photograph.

Figure 3.10 Schematic drawing of the internal structure of a chloroplast, based upon electron photomicrographs. Note the stacks of grana, which are interconnected within the stroma.



often seems to be concentrated in the endoplasm of the cell, hence the name endoplasmic reticulum (Figure 3.5). On the basis of available data, it is thought that this network is a three-dimensional continuum of cavities bounded by a membrane system. According to this view, it divides the cytoplasm into that within the network and that outside the network. The reticulum is not confined to the endoplasm, as its name might imply, but extends into the ectoplasm as well. In fact, electron micrographs indicate that the reticulum is continuous with the cell membrane at the surface of the ectoplasm and with the nuclear membrane at the outside surface of the nucleus (Figure 3.6).

In a number of cell types (especially those which are extremely active in protein synthesis), large numbers of small granules approximately 150 Å in diameter are seen to be attached to the outer membrane of the endoplasmic reticulum. These granules are called *ribosomes*. Chemical analysis of ribosomes indicates that they are composed largely of RNA and protein. Functionally, they serve as the site where amino acids are joined together in the synthesis of protein molecules.

In this connection, another term should be presented and defined—the term *microsome*. A microsome is not a structure of the intact and living cell as such. Rather, it is a term which has arisen in connection with the development of a technique for studying cells, the technique of *differential centrifugation*. In order to study subcellular particles, the biochemist breaks the cell membrane by one means or another and subjects the cell contents to high speed centrifugation. When particles of various sizes are spun in a centrifuge they migrate toward the bottom of the centrifuge tube at varying rates, depending on their mass. By this means, particles of different sizes can be isolated for further study. When cell contents are centrifuged at speeds equal to 40,000 to 100,000 times the force of gravity, the endoplasmic reticulum breaks up into particles of relatively small size, and these particles, the microsomes, migrate toward the bottom of the tube. Thus, a microsome is a product of differential

centrifugation representing a small portion of the endoplasmic reticulum with one or more ribosomes attached, and is capable of carrying on protein synthesis under experimental conditions. From a functional standpoint, the terms ribosome and microsome are often used synonymously—but they actually represent different physical entities.

The Golgi complex This organelle is a system of smooth membranes which are arranged in parallel fashion and which enclose vesicles, or cavities, of varying sizes. It is particularly conspicuous in animal cells (Figure 3.5), especially those which are active in secretory functions. This observation, plus other evidence, has led to the belief that the Golgi complex is somehow associated with secretory processes, at least in certain cells. Other lines of evidence suggest that this organelle may have other functions as well, especially in cells which are not secretory in nature. For example, it appears to be physically involved in the formation of new cell wall material in plant cell division.

It is still controversial among cytologists as to whether the Golgi complex has a separate identity from that of the endoplasmic reticulum, or whether it is continuous with it. At least from a functional viewpoint, it may be best to regard it as a part of the endoplasmic reticulum, since it resembles those portions of the reticulum which are devoid of ribosomes. However, electron micrographs indicate that it has structural features not characteristic of the endoplasmic reticulum proper, and some cytologists regard this as evidence that the Golgi complex is not a part of the general membrane system within the cell.

Lysosomes In 1955, the cytologist C. de Duve obtained a group of subcellular particles from differential centrifugation studies, which were intermediate in size between the microsomal and mitochondrial fractions. Biochemical analysis revealed that these particles were rich in hydrolytic enzymes, that is, enzymes which catalyze the digestion of large macromolecules into micromolecules. Because of their association with digestive activity, these particles were named *lysosomes* (Gr. *lysis*, loosing + *soma*, body). Apparently, the lysosomes with their hydrolytic enzymes are functional in processes of intracellular digestion. They probably account for the digestion of relatively large macromolecules taken into the cell by special transporting mechanisms. They may also function in the breakdown of cell parts whenever a cell dies. A number of electron microscope studies have confirmed the presence of these organelles in a variety of cells. Figure 3.6 shows lysosomes in relation to other parts of the cell.

Centrosphere and centrioles In many animal cells a clearly de-

defined region of cytoplasm may be observed close to the nucleus. This region is termed the *centrosphere* or *centrosome*. Within the centrosphere are located a pair of small granules, the *centrioles*, which are usually rodshaped and may be seen with an ordinary light microscope. Thin sections of cells viewed with the electron microscope show each centriole to be a hollow cylinder 300 to 500 $m\mu$ in length and approximately 150 $m\mu$ in diameter. The centriole wall around a central cavity is composed of nine separate fibrils. The two centrioles are situated at right angles to each other, as shown in Figure 3.6. The centrioles are apparently self-replicating organelles, and they play an important role in the division of animal cells.

3.4 Levels of organization As we pointed out earlier, the cell is the basic unit of living systems, and as a solitary entity, it is capable of carrying out all the activities characteristic of "living" matter. However, as one surveys the diversity of living forms, it becomes evident that in the competition for energy, higher levels of organization than the solitary cell are extremely efficient, and apparently, this accounts in large part for the successful adaptation of complex organisms in nature. Thus, cells are associated together in varying degrees of complexity and interdependence, and in many circumstances, a division of labor with regard to the intake and transformation of energy has occurred. At the highest levels of organization, such as may be found in a complex animal body, the characteristics of living systems are manifestations of highly organized and specialized cell groups.

In many of the less complex multicellular organisms, cells have become associated together in the formation of colonies with no subsequent division of labor. In other words, each cell in the colony seems to retain its separate functional identity. Such organisms are still essentially unicellular, but they represent a *colonial* level of organization. It may be that these organisms reflect a stage in the development of truly multicellular organisms, in which there is a division of labor, from solitary unicellular forms. This colonial level of organization is exemplified by many of the green algae (Section 4.4).

The next level of organization is that of a loose association of cells which exhibit a certain degree of cell specialization and division of labor. We might call this the *associational* level, and it is exemplified by the sponges (Section 4.3), where specialized cells function in such activities as digestion and reproduction. In this case, other cells do not perform these functions; they are either very generalized in this regard, or else they exhibit specializations of their own.

At a still higher level of organization (which might be termed the *tissue level*), whole blocks or groups of cells differ from other groups

both structurally and functionally. A tissue may be defined, therefore, as a group of similar cells which are associated in the performance of a particular function. This level of organization is apparent in most multicellular organisms, where a variety of different tissues may be found in a given organism. We shall consider the major plant and animal tissues in a later chapter.

Subsequent levels of organization are represented by organs, organ systems, multicellular organisms, and (in a rather special sense) groups of organisms. An organ may be defined as a group of tissues associated together in the performance of specific activities. Similarly, an organ system is a group of organs which are associated together in the performance of related activities. A complex multicellular organism, such as a human being, represents an extremely high level of organization involving integrated organ systems which exhibit the activities characteristic of life. In a special sense, the complexity of this organization is extended to groups of organisms, where a division of labor may exist. This is particularly obvious in such an insect society as a hive of honey bees.

Perhaps an analogy will serve to clarify the foregoing discussion to some degree. Let us imagine a wilderness area which has just been opened to settlement. Several families move into the area and each builds a homestead several miles from any of the others. Any given family is in virtual isolation, and is obliged to grow its own food, manufacture its own clothing, and in fact, provide for its every necessity. In time, however, other families move into the area, and the picture changes. Families in close proximity to each other realize that they can get along much better if there is a division of labor. Consequently, one man who excels at blacksmithing does this work, another raises wheat and swaps it for labor and other commodities, and so on. Eventually, with the influx of more people, an even greater degree of specialization is achieved; shops and stores concentrate on particular services, clearly defined occupations and professions arise, and in time, there is a great division of labor.*

Within limits inherent in analogies, something of the same thing has apparently happened in the world of life. At one time, evidently, all life existed in the one-celled state. Gradually, in time, the colonial and associational levels of specialization appeared, and after this, the tissue level. Eventually, multicellular organisms with organs and organ systems arose, and in general, they became the most successful organisms on earth. It appears highly probable that the

*It is always tempting to interpret nature anthropomorphically (see Section 9.5); for teaching purposes, scientists frequently employ analogies in which this attitude is strongly implied. It should be understood that such analogies are only meant to clarify some point, not to impute a form of intelligence to physical systems.

greater efficiency made possible by complex division of labor played a large part in their success, especially in their adaptation to environments not accessible to the less complex organisms.

We must be careful to avoid a particularly dangerous pitfall in thinking of development (evolution) in these terms. It is tempting to postulate some inherent, protoplasmic drive toward specialization. While we have no absolute assurance that such an inner force does not exist in protoplasm, we have no evidence that it does. Consequently, the postulation of such a force is not a very fruitful conceptual scheme to use in explaining increased complexity and division of labor over time. In a later chapter, we shall introduce the principle of natural selection, which is a very fruitful conceptual scheme indeed. Without attempting to define natural selection at this point, perhaps we can employ it as a tentative explanation of the increase in specialization that has apparently occurred over time. It is not unreasonable to assume that under some environmental circumstances a division of labor among cells enhanced survival in a world of one-celled organisms. As a matter of fact, it is possible to demonstrate this at the present time. Following this line of thought, perhaps we can visualize colonial, tissue-level, and more complex stages of specialization as imparting certain advantages to organisms in their competition with less complex forms. The question might be raised as to why these less complex forms did not disappear from the earth if natural selection explains the rise of more complex forms. This is an interesting question, and as we proceed through the remainder of the book, perhaps you can supply a satisfactory answer to it.

3.5 Summary The properties and characteristics of living systems emerge at a level of organization which is somewhat difficult to determine. However, most biologists agree that the cellular level of organization represents the least complex level which can unquestionably be called "living." At this level, there is a considerable range in size and complexity of cells themselves.

The material of which cells are composed is called protoplasm. Essentially, it is a complex, polyphasic system containing a wide variety of molecules and particles, all associated together in an aqueous medium. Although certain elements, compounds, and subcellular particles can be identified as being common to most cells, there is great diversity among living forms in this respect. Furthermore, although a great deal is known about the chemical and physical properties of protoplasm, "life" cannot be completely explained or adequately defined by these properties. It seems more appropriate to recognize the emergent properties of metabolism, growth, re-

production, responsiveness, and adaptation as characteristics of living systems than to attempt a precise definition.

The "generalized" cell includes the following subcellular particles or organelles: the nucleus, including nucleoli, chromatin, and nuclear membrane, the cell (plasma) membrane; the endoplasmic reticulum with its associated ribosomes; the remainder of the cytoplasm containing mitochondria, plastids, lysosomes, Golgi complex, centrosphere with its centrioles, and such inclusions as glycogen granules and fat droplets. Each of these is illustrated and discussed in this chapter.

A hierarchy of organizational levels is seen among organisms; this sequence consists of cells, colonies, tissues, organs, organ systems, multicellular organisms, and groups of organisms, in that order of complexity. There is some reason to believe that each level succeeded the preceding one in evolution.

Questions

1 Why is the term "life" difficult to define? If you were obliged to attempt a definition, how would you do so in terms of the second law of thermodynamics?

2 Even though some cells are said to be "very large," none achieves a size nearly approaching that of the largest multicellular organisms. Can you advance an explanation as to why cells do not become as large as elephants or, for that matter, as large as marbles? Attempt an explanation of their relatively small size.

3 A contemporary biologist, Garrett Hardin, wrote an article several years ago entitled "The Meaninglessness of the Word Protoplasm" (*Scientific Monthly*, Vol. 82, 112-120). It is well worth reading in the light of this chapter, but even if you do not have an opportunity to do so, can you guess what his viewpoint may have been? If you were asked to write an essay entitled "The Meaninglessness of the Word Life," what would you say?

4 In organisms, structure and function are often easy to correlate. For example, one might very easily determine the life habits of an eagle by examining its wings, feathers, beak, and talons, even though no observations had been made of the bird in nature. This same correlation may be made with cellular organelles. List the major organelles and particles along with their chemical and physical characteristics, and tell how these characteristics are related to function in each case.

5 Do you believe that scientists will ever create "life" under laboratory conditions? What problems might be involved in the pursuit of such an achievement?

6 There are far more amoebas in the world than there are hu-

man beings. Do you think an amoeba (a one-celled animal) is more efficient than man in competing for energy? Defend your answer.

7. What was the analogy regarding a clock and its parts meant to illustrate? What about the analogy regarding families which settled in a new territory?

8. Do you suppose that all structures within a given cell could be seen at one time? In order to verify the existence of the several cellular inclusions discussed in this chapter, what techniques would have to be employed?

9. A mature skeletal muscle cell performs all the basic functions of life except that of reproducing more muscle cells. Is such a cell alive? Defend your answer. Defend the opposing answer.

10. What are viruses, and why were they introduced in this chapter? Swanson (see reference below) says, concerning viruses, "They are living organisms, but they are not cells." The closest comparison that we can make between viruses and cells (if such a comparison is legitimate) is that the viruses are cells without cytoplasm; they possess little more than the nuclear hereditary apparatus. In what respects are viruses organisms, and in what respects are they not?

References

Butler, J. A. V. *Inside the Living Cell*. New York: Basic Books, Inc., Publishers, 1959. This small book is written in such a manner that the person of limited background can understand it. The author considers a number of cellular problems that are highly important to biology as a whole.

Gerard, R. W. *Unraveling Cells*. New York: Harper & Row Publishers, 1940. This highly readable book is a classic in biology, and will serve the student well as a general treatment on cells.

Swanson, C. P. *The Cell* (2nd ed.). Englewood Cliffs, N.J.: Prentice-Hall, Inc., 1964. This is another in the Foundations of Modern Biology series described above. The author's first four chapters are particularly appropriate to our present chapter.

Wilson, G. B., and J. H. Morrison. *Cytology* (2nd ed.). New York: Reinhold Publishing Corp., 1966. An introduction to cell biology that enlarges upon the concepts presented in this chapter.

In addition to the books listed above, attention should be called to the several excellent articles on cells which have appeared over the years in *Scientific American*. Many of these articles have been selected for inclusion in a single volume, *The Living Cell* (San Francisco: W. H. Freeman & Co., Publishers, 1965). Since that time other articles on this subject have appeared in *Scientific American*, and it is very rewarding to browse through available issues of this journal with a view toward keeping abreast of developments in cell biology.

Plant and animal diversity

In the preceding chapter we described the cell as the fundamental unit of living systems. Although biologists may study units that are either more complex than cells (tissues, systems, organisms) or less complex than cells (organelles, molecules, genetic systems), the cell is always something of a focal point. This is because life processes are essentially cellular, at least as they are considered in an organizational sense.

Nevertheless, in attempting to understand the world of life, we must ultimately study organisms themselves. In fact, even cellular characteristics differ so much from organism to organism that it frequently becomes necessary to know individual and group characteristics of organisms before the study of cells becomes meaningful. In Chapters 6 through 9, we shall relate cells to organisms in terms of fundamental activity, but before attempting to do this, it becomes necessary to gain some idea of the variety of living forms, their structural and functional relationships to each other, and some insights which have been gained through attempts at their classification. The present chapter, therefore, constitutes something of a departure from the mainstream of our thought, but we will need this information in succeeding chapters for purposes of exemplification. Hence, we feel that such a departure is justified and necessary at this point.

4.1 It is obvious that the student of living forms is obliged to develop some system both in regard to nomenclature and to classification; otherwise, his work would be aimless and chaotic. Furthermore, if his system were entirely different from those of other investigators, there would be no common basis for understanding the work of the many individuals so engaged.

**Carolus Linnaeus
and biological
systematics**

This confusing situation largely prevailed before the time of Karl von Linné, a Swedish botanist (1707–1778), who is better known by the name Carolus Linnaeus. Although some attention had been directed toward the problem by other biologists, Linnaeus was able to introduce a system of naming and classification whose major features are employed to the present day.

Essentially, this system is based on two major premises, namely, the employment of Latin or latinized names and the classification of living forms according to a hierarchy of categories ranging from the most specific groups which ordinarily need to be recognized taxonomically (species) to the most general (kingdoms). The selection of Latin as the language of taxonomy has proved to be most fortunate since it is no longer a vernacular language and, therefore, is not subject to basic grammatical changes. Furthermore, it has been employed for centuries as the language of scholarship and thus has found ready acceptance among civilized peoples. Although the

original categories erected by Linnæus and his contemporaries have been altered to accommodate an improved knowledge of organisms, the fact that the system itself remains highly workable is a tribute to its founder.

Taxonomists employ the following major categories: kingdom, phylum, class, order, family, genus, and species. Quite frequently, intermediate categories such as subphylum, superorder, and so on, are created to fill specific needs. Thus, it is the goal of taxonomy to place every organism in a species, every species in a genus, every genus in a family, and so on.

By way of illustration, let us consider the classification of an animal common to everyday experience, the domesticated cat. In distinguishing it as a kind (or species) of organism different from all other organisms, we can best start with the most general category of classification and proceed toward the most specific. There are two great kingdoms into which most organisms fit readily on the basis of characteristics that will be defined later on. These are the *plant* and the *animal* kingdoms, and our specimen is classified in the latter group. Of the many phyla which taxonomists recognize in this kingdom, we find that the cat possesses those characteristics generally accepted for the phylum *Chordata*, a group that is made to include all animals exhibiting, among other features, a structure called a *notochord* at some time during their lives. Of such animals, one group, the vertebrates, are able to replace the notochord with a vertebral column and hence comprise the subphylum *Vertebrata*. Within this subphylum, several classes are recognized. Our animal is placed in the class *Mammalia* along with all other vertebrates whose young are nourished by means of milk and who produce hair as an external body covering, to mention two of their characteristics. This class is divided into several orders, one of which, the order *Carnivora*, is made to include those mammals whose natural food is the flesh of other animals. The carnivores differ so much among themselves that a number of families have been established taxonomically, and the cat is placed with other carnivores to which it bears a strong resemblance in the family *Felidae* (the cat family). Within this family, two genera are recognized; one of these is the genus *Felis*, which includes all "true" cats. There are several species belonging to this genus: *Felis leo* ("lion cat"), *Felis tigris* ("tiger cat"), and so on. Our cat differs from these, however, in one respect that has been selected for descriptive purposes. It can be tamed, and hence it is called *Felis domestica* ("domesticated cat").

By way of summary, let us arrange the classification of the house cat according to the scheme that will be found following at the top of the next page.

Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Carnivora
Family: Felidae
Genus: *Felis*
Species: *Felis domestica*

It may be pointed out that generic and specific names constitute something of a Latin or latinized* description of an organism, the generic name being a noun and the specific name usually a descriptive adjective. Because of this emphasis on a pair of names, the Linnaean system is sometimes referred to as one of *binomial nomenclature*. In keeping with correct grammatical usage, the generic name is to be capitalized, but the specific name is not except in certain unusual instances. For emphasis, both names are italicized in print. Sometimes the generic-specific binomial is called the *scientific name*. In some cases there is no special need to cite the specific name, for example, it may not be known, or the person involved may wish to refer to a characteristic common to all species belonging to the genus. Under such circumstances, it is perfectly in order to cite only the generic name. However, a specific name should be used only in conjunction with a particular generic name.

Occasionally, it becomes necessary to recognize *varieties* or *sub-species* within a species. These categories assume considerable importance to taxonomists, but they are not ordinarily considered in classifying an organism.

It should be emphasized that taxonomic categories are abstractions since only organisms really exist in nature. Furthermore, the exact limits of these categories sometimes become rather arbitrary. A phylum is a group of similar classes, a class is a group of similar orders, and so on, but the degree of similarity required must be decided, in the final analysis, by some taxonomist. At the species level, the matter of definition becomes particularly vexing because it is at this point that terminology must bridge the abstract and the concrete. It is not enough simply to say that a species is a group of similar organisms, although this is true as far as it goes. Taxonomists have failed to supply a definition of the species which is universally satisfactory because it is not entirely an arbitrary matter. Two organisms may appear to be identical in morphology, but hidden physiological differences might be sufficiently great that they do not belong to the same breeding group, for example. At this point, it is sufficient

*Occasionally, a Greek name is used.

that the student consider a species to be a group of organisms that are sufficiently similar morphologically, physiologically, and genetically to have been thus grouped together by competent taxonomists. This is a very superficial definition, however, and will require revisions whenever one speaks of species from different standpoints.

4.2 The variety of living forms Well over a million species of animals and approximately four hundred thousand species of plants have been classified, and it is certain that there are many which have not come to the attention of taxonomists. Furthermore, new species arise from time to time, perhaps slowly but surely, and for these reasons, no system of classification is complete or absolutely up-to-date.

Even competent taxonomists cannot be expected to know more than a relatively small number of separate species and their individual characteristics. Usually, a person becomes specialized in the study of one taxonomic group, perhaps an order, a family, or even a single genus, and does not attempt to become expert in the classification of other groups. Thus, it is not possible to gain a very broad knowledge of the variety of animals and plants within a short space of time, but the student of biology should gain some concept of the major groups which are recognized. The bulk of this chapter is devoted to a survey of major groups of organisms, but before we consider such groups, let us make some observations on diversity and similarity in the world of life.

Order in diversity As we have seen, Linnæus was spectacularly successful at establishing rules for arranging plant and animal species in groups, although his approach was rather artificial according to modern standards. Today, we have greater insight into the problems of diversity, and the world of life is viewed in a much different light than was possible a century or more ago.

Two biological viewpoints have been especially helpful in understanding plant and animal diversity. The first of these is the ecological viewpoint, which has been developed largely within the past century. As we observed earlier, ecology is that field of biology which studies organisms in relation to their environment. This environment includes not only physical factors, such as light, temperature, and moisture, but other organisms as well. In a later chapter, we shall consider environment as it relates to the biological phenomenon of adaptation, but for the present, let us simply note that plant and animal diversity is directly related to environmental diversity. In other words, organisms are not distributed at random throughout the world; each species is limited by its environmental requirements.

This observation is self-evident—fishes are obviously limited to

living in water, and green plants cannot grow where there is no light source. But whatever the requirements of a given organism may be, it is not an island unto itself. It is dependent, in some way (perhaps for food or shelter), upon some other organism or complex of organisms. Ecologists speak of *webs* of organisms (Figure 10.11), and this is a very meaningful concept.

What do such ecological considerations have to do with classification? A great deal, actually; so much, in fact, that we cannot enter into the subject at this point without losing our continuity of thought. Let us merely observe that when we study plant and animal groups with a view toward learning something of the diversity which exists in the world of life, we run the risk of dissecting nature into species or other groups, thus distorting the total picture. As we consider plant and animal diversity in the remainder of this chapter, let us not lose sight of the fact that the great web of nature is an endless series of relationships among all organisms inhabiting the earth.

The second viewpoint is also one with which we shall deal at greater length in a later chapter, but which we have already introduced in part. This is the concept that species are genetically inter-related, at least remotely in time, through evolutionary processes. Only in terms of evolution does classification achieve its greatest significance; otherwise, it is largely an artificial means for arranging species.

An evolutionary interpretation of nature is a relatively new viewpoint in biology. Until the middle of the nineteenth century, most biologists regarded species in hard-and-fast terms. However, it came to be recognized that such a view of nature was untenable, and (especially within the last century) the general concept of evolution has been greatly strengthened by a variety of observational and experimental approaches to the subject.

To Linnæus, the goal of taxonomy lay in arranging categories in such a way as to allow for rapid identification of any given organism. Although this is a worthy goal and one that is still sought, the modern taxonomist attempts to relate organisms to one another *phylogenetically*, or according to ancestral history, as nearly as evidence allows him. Hence, present-day taxonomy strives to establish a *natural* system of classification wherein each category relates itself to the others according to ancestral relationships. Since it is often very difficult or even impossible to establish such relationships with any degree of certainty, a natural system is more a goal than a reality, especially above the species level.

From a practical standpoint, systems of classification still tend to be largely *artificial*, in spite of the change in emphasis that has taken place. While searching for evidences of relationship in some particu-

lar group or other, the taxonomist is obliged to formulate a tentative or working system. Nevertheless, the adoption of the "natural" viewpoint has been exceedingly profitable for biology since it has brought many areas of endeavor (for example, comparative studies of body proteins) to bear upon the problems of taxonomy which formerly were not considered. In a word, the concept of evolution gives meaning to classification, and accounts for similarities (as well as differences) among organisms. Furthermore, this viewpoint (or conceptual scheme, in terms of theory) explains the great variation that is often seen within a species. We shall see later that such variation frequently leads to new species, a process which apparently accounts for the great diversity we see in nature at the present time.

A distinction between plants and animals Most people probably never wonder how biologists distinguish between plants and animals. After all, most organisms are rather easily placed into one kingdom or the other. However, the problem is not a simple one, because there are certain living forms which are not easily classified in this respect. In the main, these organisms belong to groups known informally as the *bacteria*, the *algae*, the *fungi*, the *slime molds*, and the *protozoa*. We shall consider these groups presently, but for the time being, let us regard them as "problem children" when it comes to classifying them as either plants or animals.

Many biologists regard these organisms as neither plants nor animals, and to accommodate this viewpoint, they recognize two additional kingdoms. The kingdom *Monera* is made to include the bacteria and the *blue-green algae*. The major distinction between these organisms and all other living forms is one of nuclear structure; the cells of bacteria and blue-green algae lack definite or clearly formed nuclei, whereas cells of all other organisms possess distinct nuclei. The kingdom *Protista* is made to include algae other than the blue-green forms, single-celled fungi, the slime molds, and the protozoa (one-celled animals).

Perhaps the major advantage to recognizing four kingdoms of organisms rather than two is that the four-kingdom approach reflects natural relationships somewhat more clearly than does the two-kingdom approach. If our assumptions regarding the earliest forms of life that appeared on earth are valid, the first organisms were much like present-day monerans. Over a period of time, the protists arose as somewhat more advanced forms. Eventually, what we know today as plants and animals evolved from protistan ancestors. The four-kingdom approach to present-day variety in nature is based on the assumption that evolution has proceeded along the lines indicated in Figure 4.1.

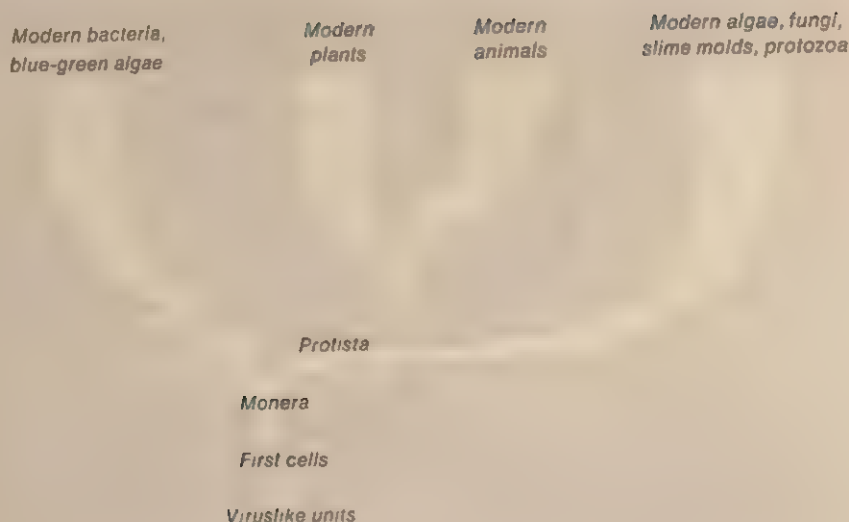


Figure 4.1 A schematic representation of one theory of how organisms evolved. This suggests that four kingdoms of modern organisms should be recognized

While recognition of the kingdoms Monera and Protista has much to recommend it, most botanists and zoologists prefer to work with two kingdoms only. Perhaps this reflects a reluctance to break with tradition, but (at least on an elementary level of studying organisms) there are probably fewer complications involved in the two-kingdom approach. We shall take this approach in our own survey of organisms, but all the while we should bear in mind that recognition of only two kingdoms is a somewhat oversimplified and artificial interpretation of organisms as they exist in nature.

Having decided upon the two-kingdom approach, we are immediately faced with a problem. How do we arrive at a single criterion or a set of criteria for distinguishing plants from animals? Will mobility do? Hardly; there are some animals (such as sponges) which are quite sedentary, and there are some plants (such as certain algae) that move about quite freely. At the very least, we would find it awkward to use mobility as a valid criterion. Perhaps we could make some distinctions on the cellular level, as we do in separating the monerans from all other organisms. For example, most higher plant cells are bounded by a rigid cell wall composed in large part of

cellulose, whereas the cells of higher animals are generally bounded only by their cell membranes. However, we run into trouble here when we consider the very organisms with which we need the most help, because great variety is seen in these "lower" organisms with regard to cell boundaries and other cellular characteristics.

Perhaps most biologists feel that, if a distinction is to be made between plants and animals, it is best made in regard to the nutrition of an organism. On this basis, we can make a fairly distinct and meaningful classification of organisms, and we can apply convenient terms that describe major modes of nutrition.

Fundamentally, animals can be distinguished from plants by virtue of the fact that animals eat and plants do not. In other words, animals take into their bodies food materials that have to be broken down into small molecules through the process of digestion before they can be utilized. An organism which gains its nutrition chiefly or entirely by eating is called a *phagotroph* (Gr. *phagos*, to eat + *trophikos*, nursing). In contrast, plants are not phagotrophic, but they exhibit two distinct modes of nutrition. As a consequence, we are obliged to recognize two distinct groups of plants. One group consists of plants which are capable of synthesizing their own food substances from carbon dioxide and water, with sunlight usually serving as a source of energy for the process. Such plants are said to be *autotrophic* (Gr. *autos*, self + *trophikos*). Other plants are dependent upon outside sources for food, as are animals, but they are obliged to receive the food in such a form that it will diffuse through cell membranes. These plants are said to be *heterotrophic* (Gr. *heteros*, other + *trophikos*).

There are some exceptions to these nutritional rules. For example, an organism called *Chrysamoeba* possesses chlorophyll and thus is capable of manufacturing carbohydrates, but it also eats solid food particles under certain conditions. Hence, it is both autotrophic and phagotrophic. The present tendency among biologists is to regard any organism that is autotrophic to any extent at all as a plant, however, and *Chrysamoeba* is generally so regarded. The slime molds are phagotrophic at one stage of their existence, but their reproductive habits are so distinctly plant-like that they are not considered animals. A few higher plants such as the Venus' fly trap (Figure 9'1), although autotrophic, capture insects for food also, thus exhibiting phagotrophic nutrition of a sort. Certain animals, particularly forms which are adapted to a parasitic habit within the bodies of other animals, may receive food from the host in such a state that it will diffuse into their bodies, and thus they are not phagotrophic. The tapeworm is such an animal. However, such forms resemble definite animal groups so closely that there is no tendency to regard them

as heterotrophic plants merely because of their nutrition. They are, rather, said to be *saprophytic* (Gr. *sapros*, decayed + *zoon*, animal).

In spite of such exceptions, which are relatively few, the characteristic mode of nutrition of an organism probably constitutes the most reliable criterion for deciding whether it is a plant or an animal. On this basis of distinction, there are very few species that cannot be definitely assigned either to the plant kingdom or to the animal kingdom.

brief survey of the animal kingdom

- 4.3 Most zoologists recognize the existence of some twenty-five or more phyla, many of which contain a relatively small number of species. Ten phyla are usually considered "major" phyla in that they include most animals which are commonly encountered and because they represent important differences among animals. As a matter of fact, approximately 99 percent of the known animal species belong to these ten phyla. Because we must restrict ourselves to a brief survey, we shall make no attempt to discuss many of the animal phyla. Some of them include animals that most of us never see and never will see. An acquaintance with the ten phyla chosen will give us a fair understanding of the animal kingdom; these are discussed below according to a general pattern of increased structural complexity.

Unicellular animals THE PHYLUM PROTOZOA (Gr. *protos*, first + *zoon*) The members of this phylum are recognizable as those animals which are unicellular. Since there is an apparent limit to cellular size, these organisms are rather small. A few forms are barely visible to the unaided eye, but most cannot be seen at all without the aid of a microscope. All are sufficiently small that they must be studied under magnification in order to determine their structural details. For this reason, they are considered *microorganisms*, as are certain unicellular plants and certain very small multicellular animals.

The several classes of the phylum are distinguished from each other on the basis of locomotion. For example, members of the class to which *Amoeba* (Figure 4.2) belongs move by extending portions of the protoplasm in one direction. Such protoplasmic extensions are called *pseudopodia*. The ciliates (Figure 4.3) move by means of numerous hair-like projections termed *cilia*, which beat in a coordinated pattern. The flagellates (Figure 4.4) exhibit one to several locomotor structures known as *flagella*. As a structure, a flagellum is somewhat longer and more complex than a cilium.

Although they are not particularly numerous in total number of species, there are more individual protozoa in the world than all other animals combined. As a matter of fact, protozoans are very



Figure 4.2 *Amoeba proteus*, three individuals shown with numerous pseudopodia extended. Note the dark nucleus in the cell at upper right, with a light contractile vacuole near it. The cytoplasm contains numerous granules. (Carolina Biological Supply Co.)

Figure 4.3 *Paramecium caudatum*. Note cilia extending from the surface of the cell. (Carolina Biological Supply Co.)

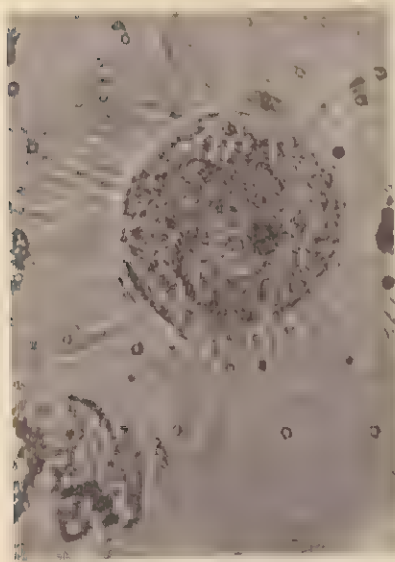


Figure 4.4 A flagellated protozoan from the digestive tract of a termite, enlarged about 500 times. Note the extremely large number of flagella extending from the cell surface; the nucleus is apparent near the center of the cell. Another flagellated protozoan of different form is seen out of the focal plane at the lower left.

widespread in nature. They are quite numerous in both fresh and salt water, and many forms grow upon or within soil. Some species are adapted to living relationally with certain higher plants or animals, for example, certain forms which cause human diseases. Several species of flagellates live within the digestive tracts of termites, where they perform the important function (for the termite) of digesting cellulose. One of these protozoa are shown in Figure 4.4.

Although protozoans are of little direct value to man, they are extremely important in the general web of life in nature. Many small multicellular animals feed on them, are themselves consumed by still larger animals, and so on, so that the protozoa are one part of a complex nutritional web. Furthermore, they are important decomposers of organic matter, in that they consume bits of decaying plant and animal materials. In a negative sense, protozoans are important to man whenever they cause diseases of the human or livestock animals. Several species of protozoa are responsible for certain human diseases; malaria, amoebic dysentery, and African sleeping sickness are examples of such diseases. From an entirely different viewpoint, they have assumed considerable importance in biological research within the past few decades. Since they are independent protoplasmic units, many of them have been used to study various phenomena of life.

Multicellular animals All animals except the protozoa are sometimes referred to collectively as the *metazoa* (Gr. *meta*, after + *zoon*), a term which has no formal taxonomic status.* In other words, the metazoa are the multicellular animals. Multicellularity introduces us to the tissue level of organization in animals, and when it arose in nature (perhaps a billion years ago), it made possible an entirely different type of animal body than would ever be possible among the protozoa. For one thing, animals with many cells can become much larger than those which exist as a single cell. Evidently, an increase in size gave the original metazoa great advantage in adapting to certain habitats, and the multicellular condition became very widespread and varied once it originated. Furthermore, the tissue level of organization gives an organism the opportunity to develop specialized structures which are hardly possible at the unicellular level of organization. As a consequence of a billion years of evolution, the metazoa have become quite numerous and varied.

THE PHYLUM PORIFERA (L. *porus*, pore + *ferre*, to bear) Members of this phylum are called *sponges*, and their bodies are perforated by pores which lead to some sort of central canal. They are really little

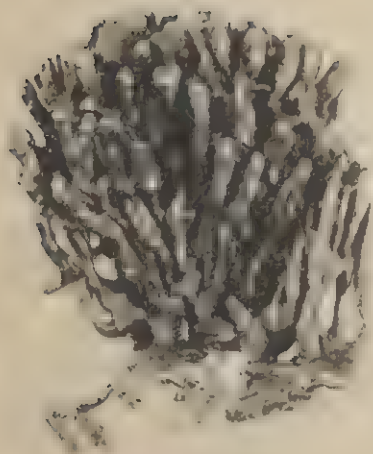
*Some zoologists separate the animal kingdom into the subkingdoms Protozoa and Metazoa, and then establish phyla under each category. We shall regard the Protozoa as a phylum, however, and the metazoa as an informal group.

more than colonies of cells which function more or less independently but which share a common skeletal structure. In some forms, the skeleton with its system of pores is capable of absorbing large quantities of water after the cells have died, which accounts for the commercial value of certain of the larger sponges.

For many years, biologists considered sponges as plants. However, it was discovered several decades ago that their cells are very similar to certain protozoa, from which they apparently evolved, and that they are decidedly phagotrophic. They certainly do not resemble any other animals; in many forms, the skeleton presents a branched appearance much like a plant body. Furthermore, they do not move about at all.

A few freshwater sponges are known, but most of them are marine. Although a few species inhabit the deeper ocean waters, most of them occupy warm and relatively shallow areas. Most sponges (Figure 4.5a) are of no commercial value, and even bath sponges (Figure 4.5b) have declined in general importance with the advent of synthetics.

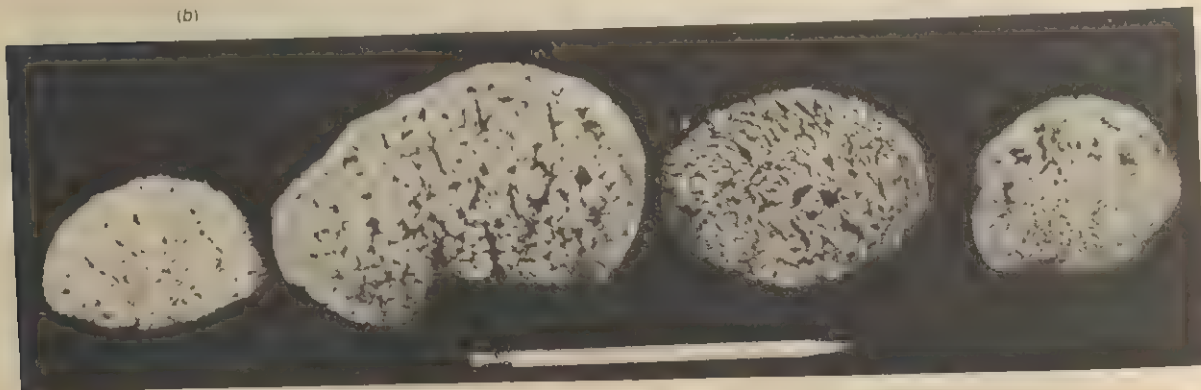
Sponges possess a very interesting characteristic that deserves some mention at this point because it is seen to at least some extent in all animals. This is the phenomenon of regeneration, which is the development of an organism from a part, or the regrowth of a lost or injured portion of the animal. We shall discuss regeneration as a special type of growth in a later chapter, but we introduce the phenomenon at this point as a characteristic of sponges. For example, a



(a)

Figure 4.5 Some representative sponges (a) A cluster of sponges as they might be seen growing on the shallow ocean floor. The entire cluster would measure perhaps a foot in height. This type of sponge has no commercial value (The American Museum of Natural History) (b) some typical spongin (bath-type) sponges (Carolina Biological Supply Co.)

(b)



large sponge can be cut into very small pieces, and if each piece is attached to some surface in the ocean, it will grow into a mature sponge. Regenerative power has been found to manifest itself in still another way. Cells of a sponge can be completely separated from each other by straining them through a fine cloth, and if they are then allowed to settle in a dish of seawater, they will come together in formation and grow into a sponge again. By varying experimental techniques, biologists have used this ability of sponges to great profit in learning more of the properties of cells as they behave in growth and development.

THE PHYLUM CNIDARIA (Gr. *knide*, sea nettle) Cnidarians, as these animals are called, show a definite advance in complexity over the sponges. For example in the cnidarians there is some grouping of similar cells in the formation of tissues, whereas the sponges are characterized by cells which are somewhat loosely associated with each other. Another manifestation of increased complexity is the presence of a greater number of specialized cell types. For example all cnidarians possess certain cells which have barbs, or stinging threads. It is for this characteristic that the phylum is named. Each of these threads carries a chemical substance which is irritating to other animals. In addition to this specialization, cnidarians are the simplest multicellular animals to exhibit a cavity where foodstuffs are broken down by chemical action, a characteristic also seen in all animals which are higher in the scale of complexity. Cnidarians possess only one opening to this cavity, a mouth, through which must pass both the food they receive and any residues of digestion that move out of the body.

Representative cnidarians are the freshwater hydra (Figure 4.6), jellyfish, and coral animals. The hydra, which abounds in fresh water ponds, is barely visible to the unaided eye. Its body cavity is surrounded by two layers of cells, some of which are specialized for contraction. In this respect, they resemble the highly specialized muscle cells of more advanced animals. This contraction enables the hydra to achieve a degree of locomotion, especially in changing the shape of its body or moving its tentacles to capture food. In addition to the contractile cells, the hydra possesses a network of nerve cells, which are specialized for the conduction of impulses. By virtue of this nerve network, it is able to coordinate its movements and respond to various stimuli.

Jellyfish range in size from microscopic forms to specimens six feet or more in diameter. Some of them are quite dangerous; the stinging cells of the larger forms are capable of paralyzing a human being. Many swimmers have drowned after having come into contact with a jellyfish.

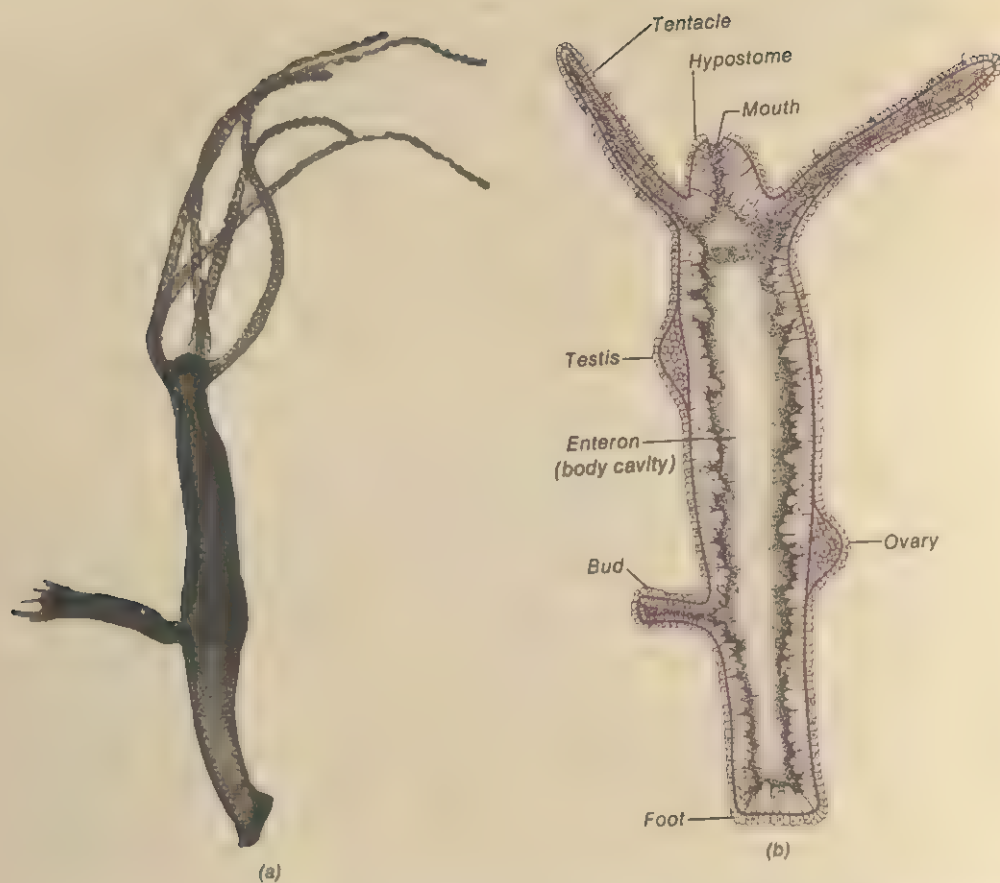


Figure 4.6 (a) Freshwater Hydra, with a bud extending from its body. Note tentacles at oral end, bulb-shaped basal disc at aboral end. The bud eventually becomes separated from the parent organism and establishes an independent existence (Carolina Biological Supply Co.) (b) Diagrammatic representation of a hydra as seen in longitudinal section.

Coral animals are quite small, and resemble freshwater hydras. Unlike hydras, however, they form colonies by secreting calcareous structures in which several thousand individuals may live. What we call "coral" (Figure 4.7) is this hard material, and it assumes varied and frequently beautiful forms. In some cases, it accumulates to such an extent that it forms large islands in the ocean.

Most cnidarians are marine, but several species (such as the hydras) are found in freshwater environments. Although they are of no particular commercial value, biologists regard them as an important group because they are the least complex animals to achieve the specialization of cells into tissues. Furthermore, they possess a high

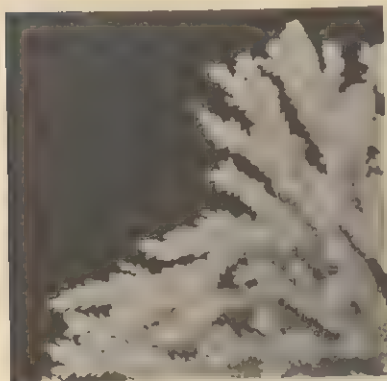
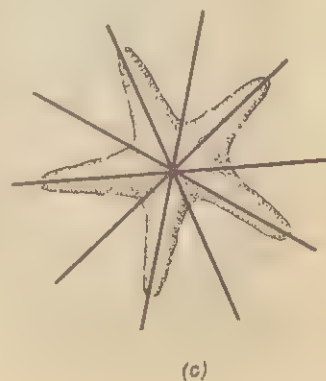
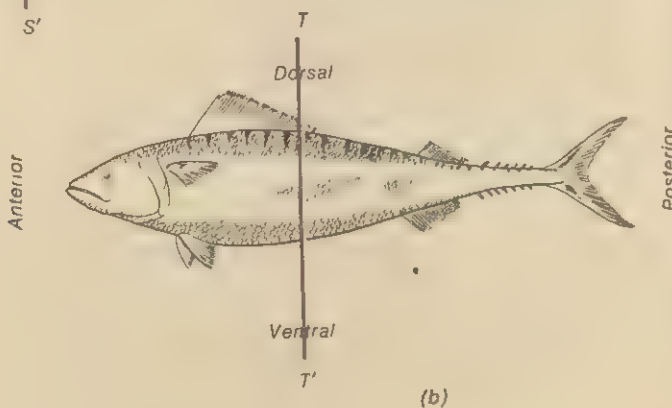
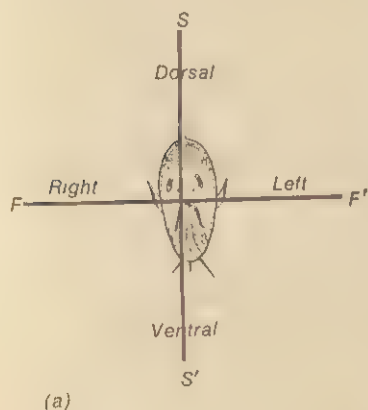


Figure 4.7 A portion of a coral formation. Originally, several hundred hydralike cnidarians occupied this formation, each within its individual "hole." The organisms have long since died, but the "coral" remains.



degree of regenerative ability, and students of animal growth and development find certain forms very useful in their researches.

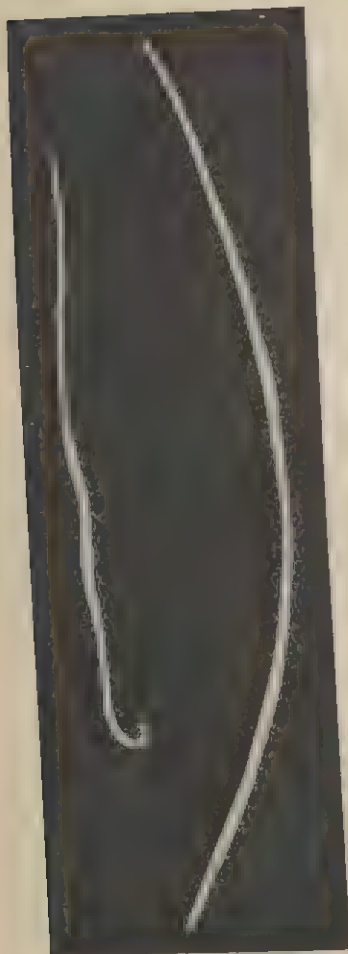
THE PHYLUM PLATYHELMINTHES (Gr. *platys*, flat + *helminthos*, worm) There are several types of animals known as worms whose body organization is such that they are elongated in the adult stage. When they move, the front, or *anterior*, end of the body leads the way, with the rear, or *posterior*, portion following along. Actually, this introduces us to a new type of body plan. Sponges and cnidarians exhibit a *radial* type of symmetry, whereas most animals higher in the scale of complexity exhibit *bilateral* symmetry. A radially symmetrical animal is built on a circular plan, much like a wagon wheel, whereas a bilaterally symmetrical animal is so organized that it can be divided by only one plane so as to produce approximate mirror images.

Such a plane (called a *midsagittal* plane) would divide the animal into left and right halves. Another plane, the *frontal*, cut at right angles to the midsagittal plane and along the axis of the body, would divide the organism into upper and lower halves. The outer surfaces of the two halves produced by a frontal plane are called *dorsal* and *ventral* surfaces, respectively. In the normal posture of most bilaterally symmetrical animals, the dorsal surface is situated uppermost, and the ventral surface is lowermost. Since man assumes an upright position, the human body is an exception to this rule even though it is bilaterally symmetrical. A plane cut perpendicular to midsagittal and frontal planes is called a *transverse* plane, which divides the bilaterally symmetrical animal into *anterior* and *posterior* portions (Figure 4.8).

Figure 4.8 A comparison of bilaterally and radially symmetrical animals (a) Sagittal (*SS'*) section and frontal (*FF'*) section as they would be described for a fish. (b) Transverse (*TT'*) section. (c) Radial symmetry as seen in a starfish.

Plant and animal diversity

Figure 4.9 Several planaria, magnified about 10 times, moving about on the bottom of a culture dish. (Carolina Biological Supply Co.)



The flatworms are the least complex of the bilaterally symmetrical animals. Their bodies are flattened dorsoventrally, which gives them a ribbonlike appearance. Three classes of flatworms are generally recognized by zoologists, one of which is composed of free-living forms. The planarian worms shown in Figure 4.9 are representative of this class. The other two classes are parasitic, and are known as *flukes* and *tapeworms*, respectively. Although free-living flatworms are of limited importance to man, the flukes and tapeworms are of considerable interest. This is because various species of each group live within the bodies of domestic animals, frequently inflicting such damage that the host animal is killed. Man himself plays host to various flatworm parasites, and they may become a major health problem in areas of the world where sanitation measures are substandard. Free-living forms are especially interesting to biologists because they are the least complex animals with bilateral symmetry. Their body systems are much advanced over those of cnidarians, and to a great extent, this difference is related to their respective types of symmetry.

THE PHYLUM NEMATODA (Gr. *nematos*, thread) Commonly called roundworms, members of this phylum are very widespread in nature. Also, a large number of species are known. Many of these worms are free-living, some are parasitic on certain plants, and others parasitize various animals. Representative of this last group is *Ascaris lumbricoides* (Figure 4.10), which may be found in the digestive tracts of the pig and man.

Roundworms are the first animals in the scale of complexity, of those discussed here, to exhibit a *tube-within-a-tube* body plan

Figure 4.10 *Ascaris lumbricoides*, a parasitic roundworm shown about one-half life size. The male is smaller than the female and has a hooked posterior end. (Carolina Biological Supply Co.)

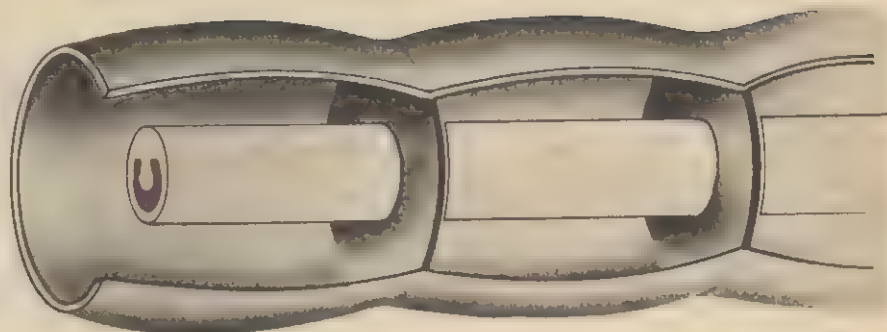


Figure 4.11 A portion of a typical tube-within-a-tube type of body. This is a diagrammatic representation of a portion of the body wall and intestine of an earthworm.

(Figure 4.11). With some structural variations, this is seen in all phyla which are yet to be discussed. Fundamentally, this type of body organization features a digestive tract with a mouth at one end and a second opening, the *anus*, serving as an exit at the opposite end. This digestive tract is the inner "tube," and a surrounding body wall constitutes the outer, there being a space or cavity between the two. This space may be occupied by body organs or fluids. Whenever such a cavity is lined with a thin tissue of mesodermal origin called a *peritoneum*, it is termed a *coelome*; if it is not so lined, it is a *pseudocoelome*. Roundworms are pseudocoelomate, while animals belonging to phyla Mollusca through Chordata, of those discussed here, are coelomate.

THE PHYLUM MOLLUSCA (*L. molluscus*, soft) This phylum is made up of animals whose soft bodies are covered with a *mantle* which secretes a firm, calcareous shell in many species. Individually, members of the phylum are called *mollusks*. They exhibit a coelome, as do representatives of phyla Annelida through Chordata, although in the case of the mollusks this body cavity is greatly reduced. Certain adult forms, of which the snails are representative, depart from the fundamental bilateral symmetry that is characteristic of the group and exhibit a coiling of the shell and other body parts. A ventral muscular mass, the *foot*, is usually present. There is a decided increase in complexity and specialization of organ systems over the phyla that have already been discussed; there are well-developed digestive, circulatory, excretory, and nervous systems.

The phylum is quite large and includes clams, oysters, snails, squids, and octopuses (Figure 4.12). These are variously and widely distributed in the ocean, in fresh water, and on land. There is great variety in form; an octopus, for example, bears little external resemblance to a clam.

From the viewpoint of man's interests, the mollusks are very important. Clams, oysters, and many other forms are edible and have

Figure 4.12 A small octopus. Note the eight tentacles with suction cups. (Carolina Biological Supply Co.)



been highly prized food items since antiquity. Pearls are sometimes produced in clams and oysters, and the shells of these mollusks are useful in the manufacture of buttons and other commodities.

THE PHYLUM ANNELIDA (*L. anellus*, a ring) *Annelids*, or *segmented worms*, exhibit a series of segments, all of which are approximately identical from external appearance, with certain exceptions. Segmentation is so strong a feature in these animals that even the internal organs reflect it to a great degree. In this respect, their bodies are built upon a plan different from those animals we have studied previously. Although most animals higher in the scale of complexity show varying degrees of segmentation, especially in their embryonic stages, the annelids are segmented to such an extent that it is considered their outstanding characteristic as a phylum.

Almost all members of the phylum bear small, nonjointed appendages called *setae*. The coelome is quite extensive (Figure 4.11), and systems are remarkably well-developed. The wide range of adaptability among members of this group is seen in the variety of habitats occupied. The most familiar annelid is the earthworm, which occupies a terrestrial habitat. A fairly common marine form is the clamworm, which is somewhat larger and more complex in external structure than the earthworm. The leech (Figure 4.13) is a common freshwater form.

With the exception of the earthworm, annelids are not of great importance to man. The burrowing habits of the earthworm render it invaluable to the farmer. Not only do its passages and tunnels permit greater penetration of air into the soil, which hastens decomposition of organic materials, but the earthworm actually eats much of the

soil through which it travels. As a consequence, organic materials are broken down very rapidly in the intestinal tract, and when the soil is eliminated from the digestive tract of the worm, it is much more suitable for growing crop plants.

THE PHYLUM ARTHROPODA (Gr. *arthron*, joint + *podos*, foot) In number of species, the *arthropods* outweigh all other animal phyla combined. They are highly successful as a group, occupying every known type of habitat and exhibiting a wide variety of body types. The characteristic around which they are grouped is the possession of paired, jointed appendages, but they exhibit many other distinctive features. There is a hard *exoskeleton* composed of a material known as *chitin*. The coelome is much reduced, somewhat as in the mollusks. Segmentation is not nearly so obvious as in annelids, but is quite marked. *Cephalization*, which may be defined as the accumulation of nervous and sensory tissues at the anterior end of the body, is evident to a degree not seen in the phyla that have been surveyed to this point. An accompaniment of cephalization is the presence of compound eyes which function in the reception of visual impulses. Body systems are quite complex and highly efficient. A number of classes and other taxonomic groups have been erected to distinguish between such forms as crustaceans, insects, spiders, scorpions, mites, ticks, centipedes, and millipedes.

Since arthropods constitute such a large and varied group of animals, let us consider some of the most important forms. Crustaceans are distinguished from other arthropods by a number of technical points, but perhaps their most obvious characteristic is the possession of a very heavy exoskeleton. Most of them are marine, but several species are found in fresh water and on land. Typical marine forms include lobsters, shrimp, and crabs. The crayfish is perhaps the most familiar freshwater form, although certain little-known but numerous small forms are widely distributed in lakes and streams. There are also a great many extremely small marine crusta-



Figure 4.13 An aquatic leech, photographed at the bottom of an aquarium. Note closely packed segments arranged serially. (General Biological Supply House, Inc.)

ceans. The familiar pill-bug, a bluish-gray animal frequently seen under damp straw or lumber, is a representative terrestrial crustacean. Many of the larger marine crustaceans, such as shrimp and lobsters, are highly prized by man as food items. In the vast food webs of nature, crustaceans play an extremely important role. A great variety of both fresh- and saltwater species consume microscopic algae, and are in turn consumed by larger animals. For example, the blue whale, which is the largest animal ever known to have lived, subsists exclusively upon a small shrimp-like crustacean. By serving as they do in food webs, crustaceans assume a role of great importance in nature.

The insects are by far the most numerous group of animals on earth. They exist in such variety of form that it is difficult to generalize about them, but there are certain features shared by all members of the group. They are distinguished from other arthropods by having three pairs of walking appendages in the adult stage, and most of them possess wings, usually two pairs. Although very few marine insects are known, they are found abundantly in virtually every other environment. Most occupy a terrestrial-aerial environment, but there are many aquatic insects. Some are found within the soil, and a number parasitize the bodies of various other animals. Insects are very important to man from a number of viewpoints. Some species, such as the honeybee and the silkworm moth, are valuable for their products. Still others are beneficial because they pollinate flowers, including those of many crop plants. In some cases, a specific insect is necessary to pollinate a given plant. Still other forms, such as the praying mantis and the dragonfly, consume quantities of undesirable insects, thus keeping their populations in check. On the negative side, a tremendous number of insects are very harmful to ornamental or crop plants. Representative of these forms are locusts, aphids, and the larvae of certain moths. Termites frequently cause great damage to houses by virtue of their affinity for wood. Certain insects, especially lice and various flies, inflict great damage upon livestock animals, and frequently carry disease microorganisms as well. Man himself is susceptible to a variety of insect-borne diseases such as malaria (transmitted by certain mosquitoes) and plague, which is borne by fleas. From one viewpoint, insects are the most successful animals on earth today, as is indicated by the tremendously large number of species. As such, they represent a constant threat to man, who must wage a constant battle in order to keep them in check.

The arachnids constitute still another group of arthropods. They include spiders, scorpions, ticks, mites, and certain less familiar forms. As a group, they differ from other arthropods in possessing four pairs of walking legs. They are also unique in certain anatomical



Figure 4.14 *Centruroides sculpturatus*, a deadly scorpion of the southwestern United States. This scorpion is usually less than 3 inches in length; yet the sting of even a small specimen may be fatal to a human being. Note sting poised above body. (Carolina Biological Supply Co.)



Figure 4.15 Two similar arthropods: (a) *Scolopendra*, a large centipede, (b) *Spirobolus*, a common millipede of the southern United States (Carolina Biological Supply Co.)

characteristics particularly with regard to mechanisms of breathing. The most numerous of the arachnids are the spiders, which are greatly feared by some people, but which are almost all completely harmless. A few scorpions, such as the one shown in Figure 4 14, are extremely dangerous, and most of them are capable of inflicting a painful sting. Mites and ticks are a major nuisance to man and domestic animals, and in addition, some species carry disease microorganisms. In general, arachnids are of limited economic importance to man. Many spiders eat insects, and are of some value in this respect. The damage inflicted by mites and ticks is, of course, a **factor of some importance**.

The centipedes and millipedes (Figure 4 15) are wormlike forms that are familiar to most people. They differ sufficiently that most zoologists place them in separate taxonomic classes, but superficially they are much alike. Centipedes can sometimes inflict a painful bite, but millipedes are completely harmless. Neither of these arthropod types are of much importance to man, although centipedes do eat certain harmful insects.

In addition to the arthropod groups discussed above, there are certain others that are less frequently encountered. As a phylum, the arthropods are very important to man, especially since they are so varied and numerous, and their role in nature is a considerable one.

THE PHYLUM ECHINODERMATA (Gr. *echinos*, spiny + *dermatos*, skin) Members of this phylum are characterized by the presence of calcareous plates or ossicles which are imbedded in the dermis, thus giving them a rough, prickly external appearance. Because adult forms are radially symmetrical and because many of the body systems do not approach the degree of complexity exhibited by most



Figure 4.16 Two common echinoderms: (a) starfish in aboral view; (b) a sea urchin in aboral view. (Carolina Biological Supply Co.)

members of the higher phyla, they were formerly assigned a much lower place in the animal kingdom. However, embryological and biochemical evidence point to a close relationship to the chordates, and most zoologists now regard them in this light. This is a good example of an attempt at natural classification, since a purely artificial approach based on external, adult morphology would place echinoderms far down the scale. As a matter of fact, zoologists rely heavily upon embryological characteristics in classifying animals since relationships are often more clearly evident during early stages than in adult forms. Echinoderms exhibit an extensive coelome and a simple nervous system but no specialized circulatory or excretory systems. One unique feature of these animals is a *water vascular system*, a sort of hydraulic arrangement which makes locomotion and certain other functions possible. The starfish is perhaps the most familiar representative of the phylum; other echinoderms are brittlestars, sea urchins, sand dollars, and sea cucumbers. All members of the phylum are exclusively marine

Echinoderms (Figure 4.16) are relatively unimportant to man, although sea cucumbers are eaten in certain areas of the world. From a negative viewpoint, starfish prey upon some mollusks which are commercially valuable. Oyster beds, for example, may be ravaged by these echinoderms, and they do sufficient damage that oyster fishermen attempt to eradicate them. In earlier times, starfish were removed from oyster beds by dragging long mops across the shallow ocean floor. The starfish grasped the threads by using small pinchers embedded in the body wall, and were pulled out of the water. Before they learned better, the fishermen chopped the starfish into two or three pieces and threw them overboard. Because of their considerable powers of regeneration, the starfish frequently became more numerous after such an operation. After this became apparent, the starfish were killed by drying them on beaches, and still later, chemical methods were developed for killing them in the water.

Although echinoderms are of little value to man as items of commerce, they have served biological research quite well. Echinoderm development is similar to that of chordates, and since the embryos develop in open water, their developmental stages may be observed quite readily. Some of the classic experiments of embryology have been performed with echinoderms. Furthermore their regenerative abilities have been quite useful in biological research.

THE PHYLUM CHORDATA (L. *chorda*, cord) Long after the animal phyla which we have discussed to this point had become established on earth, there arose a group whose body structure was unlike that of other animals. These were the chordates, and according to evidences from paleontology, they originated some 500 million years

ago. Although they retained some of the more successful features of their ancestors, such as bilateral symmetry and a degree of segmentation, they exhibit three distinct structural features which are unique:

1 In their embryonic development, a group of cells form a stiff rod just beneath the dorsal body surface. This rod is called a *notochord*, and the phylum derives its name from this structure.

2 *Gill clefts* form at the anterior end of chordate embryos. In aquatic forms, these open to the outside and become passageways by means of which water passes to the gills. Among the terrestrial forms, the clefts do not ordinarily progress this far, but become modified into other structures.

3 Due to the mode of nervous system development, the main nerve cord is dorsal, lying just above the notochord, and is tubular. This is in contrast to the ventral, solid nerve cord of most nonchordates.

In addition to these three fairly clear-cut distinctions, there are certain other features which distinguish chordates from members of other phyla. Nervous, muscular, skeletal, circulatory, excretory, and reproductive systems reach a high point of specialization. In fact, as one studies the comparative anatomy and physiology of chordates, a pattern of increasing complexity appears from the most primitive to the most recent groups. In most cases, a given system shows definite signs of progressive modification, which is a strong indication of genetic kinship and evolutionary change from one form to another.

There are two distinct groups of chordates. The first of these are the *protochordates*, in which the notochord never becomes replaced by a vertebral column. One of the common protochordates, *amphioxus*, is shown in Figure 7.5. The second group (by far the larger) are the *vertebrates*, in which a series of vertebrae either partially or completely replace the notochord. The vertebral column is a part of the endoskeleton of vertebrates. None of the protochordates are very important to man, and if it were not for their biological significance as they relate to the vertebrates, we would probably consider them a very insignificant group of animals indeed.

The vertebrates are quite another matter. Although they are by no means the most numerous group in the animal kingdom as regards either total numbers of species or of individuals, they represent something of a high point in phylogeny. Because the different classes or subgroups of the vertebrates include animals which are probably of greatest interest to most of us, we will discuss the seven taxonomic classes usually recognized by zoologists.

Class Agnatha (a-, not + Gr. *gnathos*, jaw) This is the first of three classes usually recognized by zoologists as being *fishes*, which



Figure 4.17 A lamprey. Note the seven openings near the anterior end, which allow water to pass over the gills. The ventral mouth is not seen in this view. (Carolina Biological Supply Co.)

are restricted to water. As an adaptation to their environment, all fishes possess *gills* which enable oxygen to pass from the water into the blood stream. The agnatha derive their name from their failure, unlike other fishes, to develop jaws; the mouth is a round, suctorial opening. Although there is a poorly developed cartilaginous vertebral column, the notochord persists throughout life.

The lamprey (Figure 4.17) is the most common agnathan, and it is often called the lamprey 'eel.' This is a misnomer, because eels are osteichthians, or bony fishes. Lampreys are edible, although they are not highly prized for food. Since they and other agnathans attack and kill more valuable fish, the entire group is undoubtedly more harmful than beneficial to man's interests.

Class *Chondrichthyes* (Gr. *chondros*, cartilage + *ichthys*, fish). Although members of the preceding class exhibit cartilaginous skeletons, and cartilage comprises a part of the adult skeleton of many higher vertebrates, including man, this characteristic has been selected as a basis for separating this class from those fishes which possess bony skeletons. The notochord is present in adult forms, but it is greatly modified by the vertebral column.* Most members of this class are marine. Sharks, skates (Figure 4.18), and rays are perhaps the best known cartilaginous fishes. Certain sharks attain considerable size; whale sharks sometimes reach a length of fifty feet and are the largest fishes (not the largest aquatic vertebrates) known. As a group, sharks tend to be rather vicious animals, and are a threat to human life, especially if a swimmer is losing blood. Some rays are capable of delivering a powerful electrical shock, and can thus cause injury to a swimmer. Other rays possess a sting beneath the tail, with which they are able to incapacitate a human being. Chondrichthians are not particularly valuable to man, al-



Figure 4.18 A skate, dorsal view. (Carolina Biological Supply Co.)

* Although every chordate exhibits a notochord during embryonic life, this structure becomes less and less prominent in adult forms as one ascends the vertebrate scale of complexity. It is more reduced in the bony fishes, discussed below, than in chondrichthians, still more reduced in amphibians, and most reptiles retain no trace of the notochord as adults. In all birds and mammals, the notochord is replaced entirely by a vertebral column during embryonic development.

though the meat of certain sharks and rays is edible, and shark liver may be processed for the oil it contains. Because these animals destroy large numbers of crabs, lobsters, and valuable fishes, they are usually considered more harmful than beneficial from man's viewpoint.

Class Osteichthyes (Gr. *osteon*, bone + *ichthys*) Members of this class exhibit skeletons that are largely composed of bone, and for this reason they are called the *bony fishes* to distinguish them from members of the preceding two classes. A large number of species have been described, of the 50,000 or so species of vertebrates that are known, over half are members of this class. There are a number of structural differences between bony fishes and those described above, many of which are quite obvious. However, there is considerable variation in external morphology. In these fishes, the gills are covered by a plate, the *operculum*, which functions in passing a current of water over the gills. Another outstanding structural feature is the presence of a *swim bladder*, which arises as a ventral outpushing of the pharynx. This organ serves to regulate hydrostatic pressure, which helps to maintain buoyancy, and in certain unusual forms, the lungfishes, it has a limited function as a lung. Although the majority of species are marine, a large number occupy fresh-water habitats, with a few being able to exist in either type of environment.

As a group, the bony fishes are far more valuable to man than the agnathans and the chondrichthians. The economies of several countries are based on fishing, and about 10 million tons of fish are harvested each year from the waters of the world. Actually, man has hardly begun to tap the full potential of the ocean and fresh waters in this regard. As the world's population increases, and with greater understanding of aquatic biology, we will undoubtedly turn more and more to water as the medium in which to grow our food.

Class Amphibia (Gr. *amphi*, both + *bios*, life) Of the seven vertebrate classes usually recognized by zoologists, three include aquatic animals (the fishes) and three are composed of animals that are primarily terrestrial. An intermediate group, the Amphibia, shows strong similarities to both the aquatic and the terrestrial animals. For example, amphibians are aquatic during their early stages, at which time their gaseous exchange is accomplished by means of gills. Later on, most develop lungs and live on land. They differ from fishes in a number of points: legs are developed in place of fins and (unlike fishes) they do not have scales. Internally, a number of modifications to a terrestrial environment have taken place. The two-chambered heart of fishes is replaced by a three-chambered heart in amphibians, which makes for greater effectiveness of blood circula-

Figure 4.19 *Ambystoma maculatum*, the spotted salamander. What differences exist between this animal and a lizard? (Carolina Biological Supply Co.)



tion to the lungs. The most common amphibians are frogs, toads, and salamanders (Figure 4.19).

As a group, amphibians are of little importance to man, although larger forms are sometimes eaten. Toads are beneficial in gardens, because they eat harmful insects. To the biologist, amphibians are of special interest because of their intermediate position between the fishes and the land animals. Frogs and salamanders offer certain advantages as research animals, and they are thus widely used.

Class Reptilia (*L. reptum*, to creep) Reptiles derive their name from the feature that they are relatively slow-moving animals, with the snakes failing to exhibit appendages at all. They may be distinguished as a group from the Amphibia by their possession of scales and claws, which Amphibia do not exhibit. Perhaps these are the most obvious structural differences between the two groups. A number of anatomical, embryological, and physiological traits are sufficiently unique to delimit them as a class. For example, the heart is four-chambered, as is true of all land animals, although in the case of most reptiles, the two upper chambers of the heart are not completely separated. Typical reptiles are lizards, snakes, turtles, alligators, and crocodiles.

Reptiles are relatively unimportant to man, although in certain areas of the world, some species constitute a menace. Certain species of snakes are poisonous, especially some marine and tropical forms. In some areas, alligators or crocodiles are sufficiently large and numerous that they become quite dangerous. On the whole,



Figure 4.20 The duckbill platypus, an egg-laying mammal. (New York Zoological Society.)



Figure 4.21 A kangaroo with young in pouch.
(New York Zoological Society.)

however, reptiles are simply a group of interesting animals whose place in nature is not nearly so important as it was 150 million years ago, at which time they were the dominant vertebrates on earth.

Class Aves (*L. avis, bird*) Since birds are feathered bipeds, it is not difficult to see why they are rather definitely set apart from other vertebrates as a class. In addition to these features, most of them exhibit forelimbs that are adapted into wings for flight, and there are many other structural modifications which are accompaniments of this unusual ability. For example, the bones of birds are very light, with large central cavities, and the breast muscles are highly developed. Unlike all other animals which have been discussed to this point, and like the mammals which are introduced below, the body temperature of birds does not vary with the environment. For this reason, they are often said to be "warm-blooded," a term which is somewhat misleading. A lizard living in the desert, for example, whose body temperature changes with its environment, might have a higher temperature than a bird or mammal living in the same area. The class is a varied and highly successful one, and a number of different orders are recognized.

As a group, birds are of considerable importance to man. Chickens, ducks, and geese have for centuries served as important sources of meat and eggs. Various species of birds consume large numbers of harmful insects, thus helping to keep them under control.

Class Mammalia (*Gr. mamma, breast*) This class of vertebrates has been named for one of its most outstanding characteristics,

namely, that the young are nourished during early stages of post-natal life by milk secreted from mammary glands. The production of hair, which occurs in varying degrees among species as an external body covering, is also a distinguishing characteristic. Except for one primitive group, they are *viviparous*, giving birth to more or less well-developed young, whereas other vertebrates are *oviparous*, producing eggs varying in size but all of which are relatively large as compared with those of mammals. Body systems reach the acme of morphological and physiological complexity in this group, the nervous system in particular becoming highly specialized. The human species derives its supremacy largely because the nervous system of man is the most highly developed in the animal kingdom. A great deal of variety exists among mammals, as exemplified by the monotremes (Figure 4.20), the marsupials (Figure 4.21), the bats (Figure 4.22), the aquatic forms such as whales and porpoises, and the primates, of which man is a member, to mention only a few outstanding forms.

Without doubt, mammals are more important to man than any other group of animals. Long before history had been recorded, man had domesticated such animals as the horse, the dog, and the cow. In fact, it is remarkable that man has domesticated no additional important animals that he did not have 5,000 years ago. Those mammals from which we obtain food products are most important.

By way of summary, let us represent graphically some of the features of the ten phyla which we have introduced. It will be seen (Figure 4.23) that there is a gradual increase in complexity from the Protozoa to the Chordata and that successful adaptations tend to "accumulate." In a metaphorical sense, it is as though nature experimented and found that some things work and others do not. Those that do, she retained. As we shall emphasize later, evidence is overwhelming that the various animal groups arose on earth at different times, with a given phylum preceding another in almost direct pro-



Figure 4.22 *Myotis*, the brown bat, shown in flight. (New York Zoological Society.)

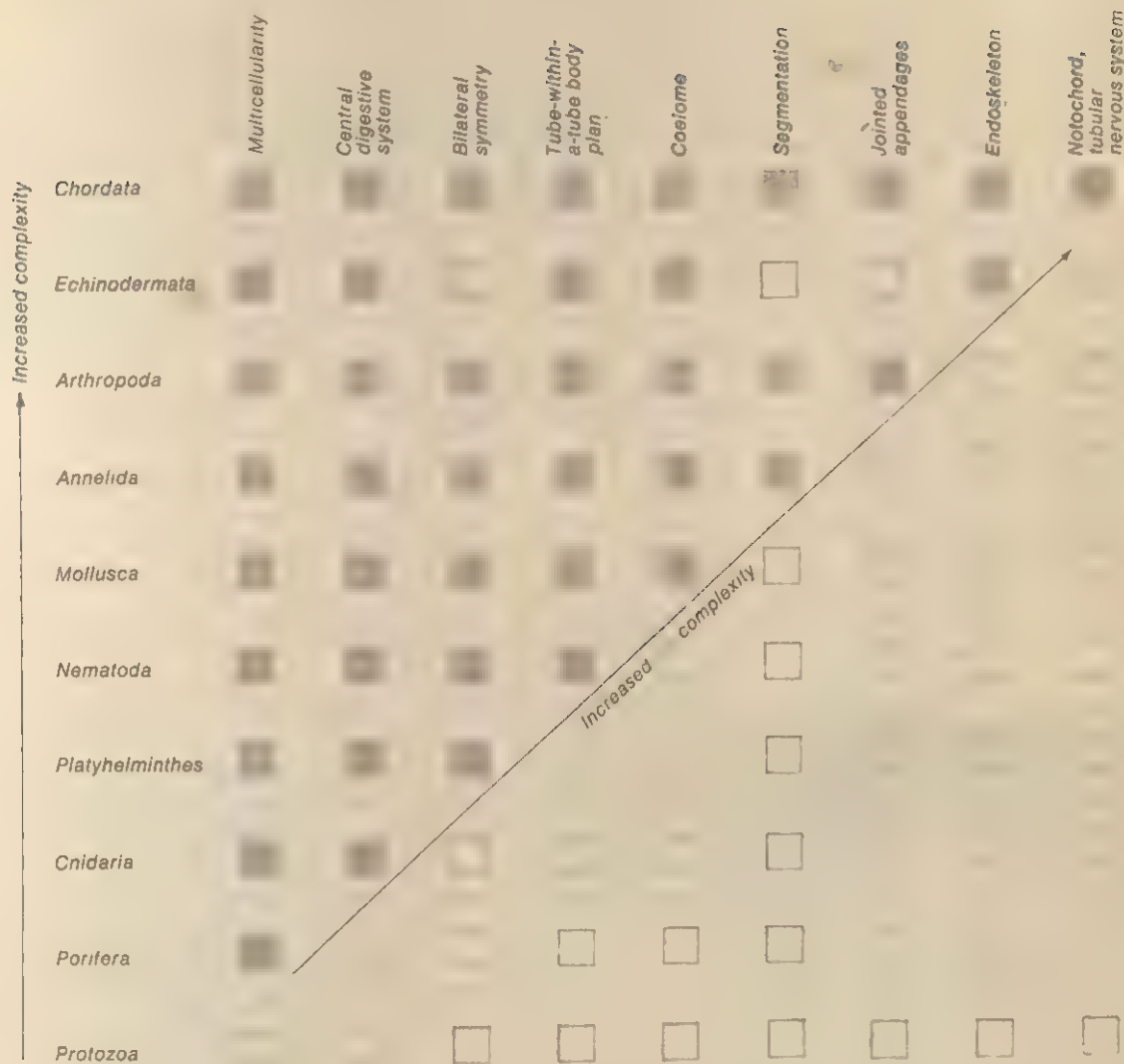


Figure 4.23 Graphic representation of the accumulation principle with regard to several important features of animals. Open squares mean "characteristic lacking," shaded squares mean "characteristic present." As pointed out in the text, members of the phylum Echinodermata deviate from the general trend in certain respects.

portion of time to degree of complexity. That some of them arose from others or from ancestors common to all is strongly indicated by all lines of evidence, and the accumulation principle is simply a reflection of an evolutionary process.

A brief survey of the plant kingdom

- 4.4 Botanists have experienced considerably greater difficulty in establishing major plant divisions* which are generally accepted than zoologists have for animal phyla. This is because evidences of phylogenetic relationships between plants and plant groups seem to be far less convincing, in general, than those which have been elucidated for the animal kingdom. For many years, four plant divisions were recognized: division Thallophyta, which included the algae, fungi, and lichens; division Bryophyta, the mosses and liverworts; division Pteridophyta, the ferns and their "allies"; and division Spermatophyta, the seed plants.

Botanists have long recognized, however, that these groups are highly artificial. Hence, a tendency has developed toward the establishment of many plant divisions or phyla in the belief that this represents a more natural type of classification when viewed from the standpoint of present knowledge regarding plant relationships. At best, however, agreement among botanists as to just how many major divisions or phyla should be recognized is by no means as complete as it is among zoologists for the animal kingdom. In view of this, it is considered best in this text to present a brief survey of the plant kingdom in terms of seven plant groups. It should not be thought that these represent formal taxonomic categories; they merely serve as a convenient system by means of which some understanding of the plant kingdom may be gained.

Algae These plants, which are relatively simple in structure and whose cells possess the green pigment *chlorophyll*, are widely distributed in nature. They grow most abundantly in marine and freshwater habitats, but they also occur in and upon soil. They are present within or upon the bodies of certain plants and animals, in hot springs, in icy puddles, on rocks, and on wood. Some are unicellular, while others grow as long chains of cells. Still others are fairly complex organisms whose cells may be arranged in various patterns. A few algae reach a considerable degree of size and complexity, but most species are microscopic.

The algae are distinguished from other autotrophic plants chiefly by their relative simplicity of form and structure. Very few algae have specialized parts that resemble the roots, stems, leaves, and reproductive structures of higher plants. Taxonomically, at least eight phyla or divisions are usually recognized; we shall discuss a few of

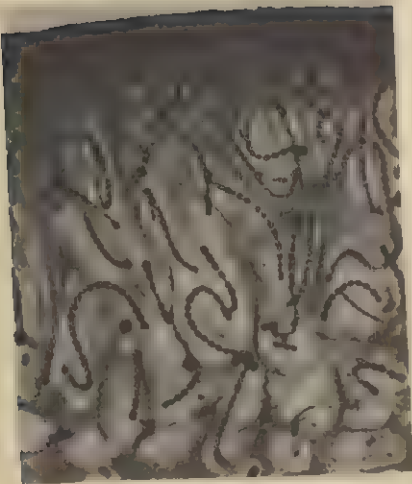


Figure 4.24 Microscopic view of *Nostoc*, a blue-green alga. The cells of this plant grow in chains, which are imbedded within a gelatinous ball in this species. The top edge of the ball is shown here in sectional view. (General Biological Supply House, Inc.)

*Botanists have traditionally preferred the term "division" at this level, thus lending to the term "phylum" a zoological connotation. However, many modern botanists have abandoned this distinction, and their systems of classification employ phylum as the major taxonomic category.

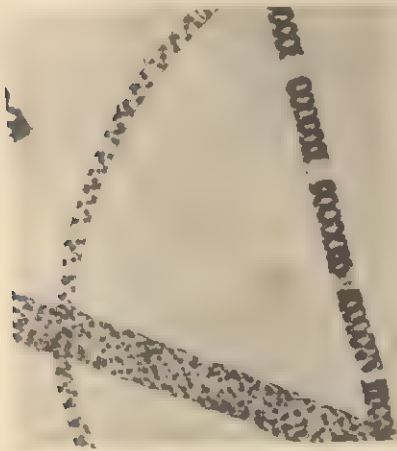


Figure 4.25 Filaments of *Spirogyra*, a common green alga found in ponds. Notice that the cells of the curved filament possess a single spiral chloroplast each, those of the right-hand filament possess two chloroplasts each, and the large filament is characterized by cells containing several chloroplasts.



Figure 4.26 *Fucus vesiculosus*, a brown alga. This plant is marine and is found attached to rocks exposed to view by low tides. (General Biological Supply House, Inc.)

these below under their descriptive group names.

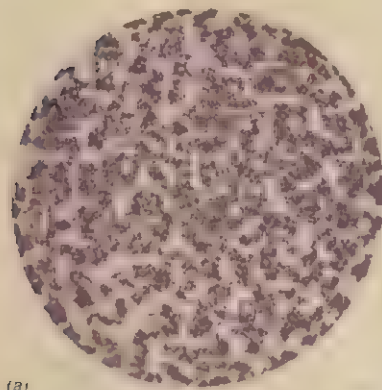
The *blue-green algae* possess certain red and blue pigments in addition to chlorophyll, and as a result, they look bluish or dark green. They are frequently abundant on the surface of soil and in waters heavily contaminated by sewage. Their cells do not have discrete nuclei, which is rather unusual; instead, chromatin is present throughout the cell. For this and other reasons, the blue-green algae are among the least complex of all living organisms. A rather common filamentous type is shown in Figure 4.24.

The *green algae* are among the most widespread and numerous of all the algae. Because chlorophyll is their most obvious pigment, they are typically grass-green in appearance. A number of different forms of green algae are known; there are many unicellular species, certain of which achieve motility by means of flagella, while others are filamentous, colonial, or even more complex. Unlike the blue-green algae, their cells exhibit nuclei, as do those of all other plants. As in most other plants, the cells of green algae have walls composed chiefly of cellulose, and the chlorophyll is concentrated in structures called chloroplasts. Most waters, both salt and fresh, abound in green algae. The characteristic greenish hue of many bodies of water is due to the presence of large numbers of microscopic forms. Quite frequently, ponds become choked or covered with masses of filamentous types such as that shown in Figure 4.25.

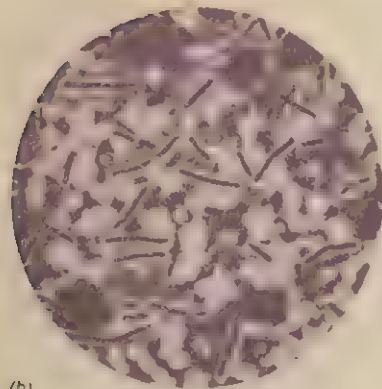
The *brown algae* are so called because of their characteristic coloring, which results from the presence of a brown pigment. Chlorophyll is also present, but it is masked to a great degree, so that these plants frequently appear to be dead or decaying. The brown algae are almost exclusively marine; they are widespread in the oceans, and many of them achieve a degree of size and complexity that is unusual for algae. In fact, some of the giant kelps ("sea-weeds") rival trees in size. One of the "rockweeds" native to the coast of New England is shown in Figure 4.26.

The *red algae* possess a red pigment in such abundance that it masks the chlorophyll, hence the common name. Some representatives are not red, but are included within the group because of other characteristics. The group is predominantly marine but there are a number of widely distributed freshwater forms. Most are filamentous, but some exhibit a broad, foliaceous organization. In general, they live anchored to the ocean floor or to objects in the water. Many forms are rather large as algae go, but none rivals the larger brown algae in this respect.

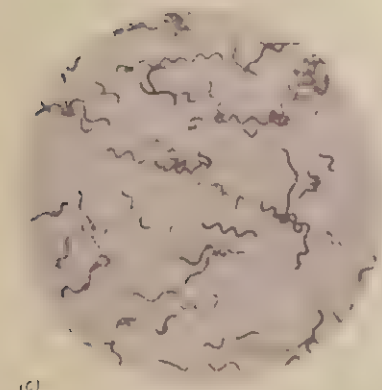
Although these four major groups include most species of algae, there are many commonly encountered forms which represent still other types. The algae comprise a quite varied group and a very



(a)



(b)



(c)

Figure 4.27 Three morphologically different types of bacteria, magnified about 1,000 times: (a) cocci; (b) bacilli; (c) spirilla. (General Biological Supply House, Inc.)

important one from the standpoint of ecological balance in nature. Large numbers of algal species serve as producers in the complex food webs that exist in aqueous environments. Since algae are autotrophic, they build up their populations from water, carbon dioxide, and mineral substances. Small fishes and crustaceans consume algae and thus build up their populations. These primary consumers, in turn, are eaten by still larger animals, and so it goes throughout the nutritional web. As a consequence of the ability of algae to build up organic substances from inorganic materials by using the energy of sunlight, a vast number of organisms are maintained in nature. Although green land plants also serve as producers in that environment they do not equal the algae in this role. About three-fourths of the earth's surface is covered by water, and about four-fifths of all primary synthesis is carried on by algae. Thus, the algae are the major producers in the overall food web.

Aside from this very important role in nature, certain algae are directly beneficial to man. Some species are edible, and a great deal of research is presently being conducted to increase the utilization of algae in this respect. Without doubt, the algae constitute a potentially important and largely untapped source of food for human beings. Even now, certain algae are part of many peoples' diets. Many species of algae are valuable in other respects. For example, a material called agar-agar, processed from certain red algae, is widely used in laboratories for the preparation of media used in growing microorganisms. Algin, from certain brown algae, is used in the preparation of some foods (for example, ice cream and puddings) as a stabilizer of colloidal particles.

Fungi Members of this group are relatively simple in structure as compared with plants belonging to those groups which are yet to be discussed. In this respect, they are similar to the algae, from which they differ as a group in being devoid of chlorophyll, a characteristic that renders them dependent upon organic compounds as a source of carbon, rather than upon carbon dioxide, which algae and all green plants are able to utilize.*

Although fungi are widespread in nature, most people are probably unaware of their presence or of their importance. Of course, mushrooms and other obvious forms are well-known, but the smaller types usually escape notice. The major types of fungi are presented below according to a general pattern of increasing complexity.

The *bacteria* appear to be the simplest of all organisms from a purely morphological standpoint, although there are certain forms,

* A few species of bacteria are autotrophic, as are green plants, but the vast majority of fungi are heterotrophic.

the "higher" bacteria, which become relatively complex in their growth and development. Most bacteria exist as small, unicellular spheres (*cocci*), rods (*bacilli*) or spirals (*spirilla*) as shown in Figure 4.27. Because of their ubiquity and their varied physiological habits, they assume tremendous importance to man and to all other organisms. Perhaps the most notable distinction between bacteria and other fungi is a cellular one; nuclear material in bacterial cells is rather atypical, a definite nucleus being difficult to demonstrate by the use of ordinary nuclear staining techniques. In all other fungi, nuclei are readily demonstrable within cells.

Some bacteria are parasitic, and thus derive their organic compounds from a plant or animal host. Whenever parasitic bacteria cause disease, which is frequently the case, they are said to be *pathogenic*. Many human diseases, such as pneumonia, diphtheria, and typhoid fever, are caused by pathogenic bacteria. In this respect, bacteria assume great importance to man. However, there are many useful species which are utilized directly by man in the production of food, medicine, various chemical substances, and fertilizer. In nature, bacteria perform a very important function. They are active in

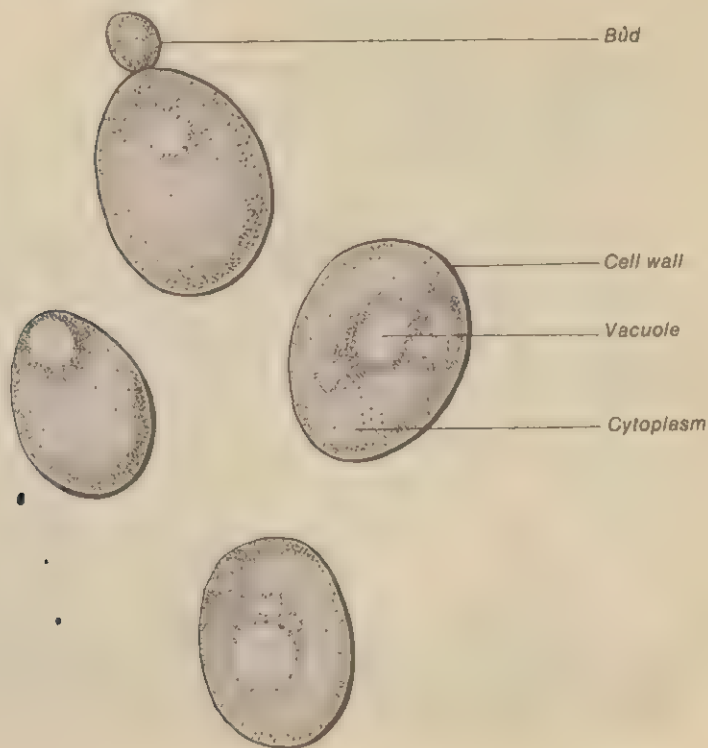


Figure 4.28 A drawing of some typical cells of common baker's yeast, showing bud production.

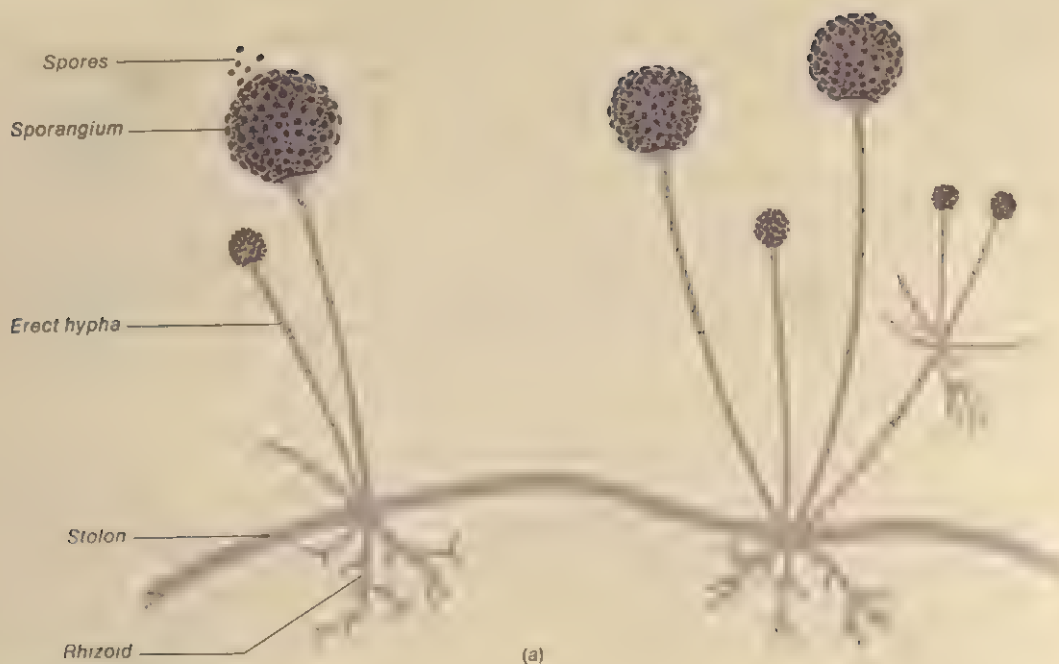


Figure 4.20 *Rhizopus stolonifer* the black bread mold. (a) Drawing of this mold showing several structures (b) Appearance at about 100 magnifications.

the decomposition of organic materials, and thus make such elements as carbon, nitrogen, and oxygen available for utilization by higher organisms. Everything considered, the usefulness of bacteria to man in this regard outweighs the harm some of them do him in the production of disease.

Another group of unicellular fungi, the yeasts, are considerably larger than bacteria, and exhibit certain morphological features which distinguish them from other fungi by appearance alone (Figure 4.28). Many yeasts are commercially important to man because of their ability to ferment sugars with the production of ethyl alcohol, which makes them important to the beverage industry. Furthermore, ethyl alcohol is widely used as a medical preservative agent and is employed in a great variety of industrial processes. Like all heterotrophs, yeasts produce carbon dioxide in their metabolic processes, and this characteristic makes them valuable to the baking industry, since bread "rises" whenever yeast cells are growing within the dough. Carbon dioxide produced by yeast may be pressurized and combined with water to form carbonic acid, which is used in the manufacture of soft drinks. Yeast cells themselves are a very important source of vitamins, and are sometimes included in livestock feeds. They are also processed for human consumption, and some people eat yeast directly as a vitamin source.

Certain fungi are characterized by filaments which form elaborate branching systems (*mycelia*) and as a consequence, they are often fuzzy in appearance. Among these mycelial forms are molds (Figure 4.29), mildews, rusts, and smuts. The molds and mildews are of considerable economic importance to man, both positively and negatively. A number of molds are useful in the manufacture of food and medicinal products, and certain forms have become extremely valuable in genetical and biochemical research. On the other hand, molds are frequently involved in food spoilage, and both molds and mildews attack valuable crop and ornamental plants, cloth, leather, and other materials upon which they are able to grow. A few mold-like plants are pathogenic to man, and cause certain diseases of the respiratory tract and the skin. Rusts and smuts are parasitic on higher plants, particularly the cereal grains. They often inflict sufficient damage to constitute a severe agricultural problem.

Certain fleshy forms, notably the *cup fungi*, *mushrooms* (Figure 4.30), and *puff balls*, are widely distributed in nature and some of them achieve considerable individual size as compared to the microscopic aspect of most fungi which have been discussed to this point. Actually, the fleshy structure characteristic of a given species is only one part of a fairly complex reproductive cycle, its development having been preceded by what is frequently a long period of activity on the part of mold-like filaments. Once started, the fleshy body may enlarge at an incredibly fast rate, a phenomenon that has made the mushroom a symbol for rapid growth. These *fruiting bodies*, as

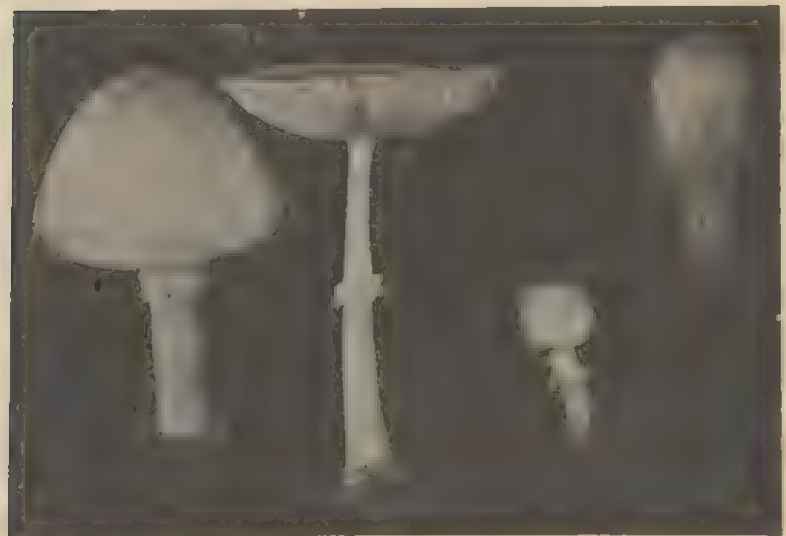


Figure 4.30 *Amanita*, a poisonous mushroom. Fruiting bodies are seen in various stages of growth. (General Biological Supply House, Inc.)



Figure 4.31 Typical lichen growth on the bark of a tree limb. (Carolina Biological Supply Co.)

botanists call them, are producers of great numbers of spores, which are reproductive cells. A few species of fleshy fungi, including mushrooms, are edible and can be grown as a marketable food item.

As a group, the fungi occupy a position of considerable importance in the world of life because of their mode of nutrition. In one sense, they occupy a position opposite to that of the algae in a nutritional "spectrum." Just as the algae are important as producers, so the fungi are important as decomposers. We have already emphasized the role of bacteria in this regard. Although bacteria are generally the most effective decomposers in nature, all fungi carry on heterotrophic nutrition, and hence break down organic compounds. By virtue of their chemical activities, elements and compounds are released to be used again by some organism.

Lichens Although lichens constitute a relatively small plant group, they deserve special mention because of their unusual nature. A lichen is a dual plant, being a sort of cooperative enterprise between an algal and a fungal component. The species thus involved form a plant body which differs in appearance from either algae or fungi, and because a given lichen reproduces itself consistently, it is considered a true species in its own right. The relationship between the alga and fungus which compose a lichen is not completely understood, but in some habitats it enables both to do together what neither can do alone since lichens thrive in a great many places where other plants do not exist. They may be found growing on rocks, which they gradually decompose, and on the barks of certain trees (Figure 4.31). Some species grow in arctic regions where few other plants are found. In the general economy of nature, lichens assume a position of some importance in the formation of soil and in serving as a source of food for certain animals which live in extreme northern regions. Because of their unusual nature, lichens have proved to be of value in some types of biochemical research.

Liverworts These plants, which are not widespread in nature, are usually restricted to moist, shaded areas, and a few grow in shallow freshwater habitats. Typically, they form a flat, green carpet on damp soil. Some, but not all, are lobed in such a way that they bear faint resemblance to the human liver (Figure 4.32). This gave rise long ago to their common name. Wort (pronounced *wurt*) is an old name meaning plant. As is true of plants which are morphologically more complex (the mosses, ferns, and seed plants), they possess chlorophyll and hence are not dependent upon other organisms for organic compounds.

Although liverworts are of no economic importance to man and play a very minor role in the total economy of nature, they are quite significant to botanists. This is chiefly because they are the least

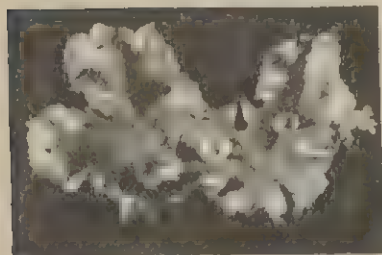


Figure 4.32 *Marchantia*, a liverwort. Living specimens are bright green in color. Note lobed branching. (Carolina Biological Supply Co.)



Figure 4.33 *Polytrichum*, a moss. The leafy portion of each plant is the gametophyte, and the stalked portion is the sporophyte. (General Biological Supply House, Inc.)

complex plants, as a group, to exhibit a dimorphic life cycle * Such a life cycle is also characteristic of the mosses, ferns, and seed plants, and we shall devote some attention to it in a later chapter devoted to the study of reproduction. Essentially, a dimorphic life cycle is an alternation between a spore-producing plant or plant part, the *sporophyte*, and a gamete-producing plant or plant part, the *gametophyte*. Typically, germination of a spore produces the gametophyte, which produces sex cells, and the fusion of two sex cells starts the growth of the sporophyte † In liverworts, the gametophyte is far larger and more conspicuous than the sporophyte, which is attached to the gametophyte throughout its existence.

Mosses Liverworts and mosses are much alike; they are both relatively small and are usually found in moist surroundings. However, mosses are more widespread in nature than liverworts, and in general, they require less water. A few mosses grow in water, but most species are terrestrial. Some grow on trees or rocks, especially where small amounts of soil have accumulated. Mosses are rather important in nature, at least in certain areas, because their growth prevents soil erosion. Some forms are useful to man as packing materials, and peat moss (*Sphagnum*) is widely used in horticulture to increase the acidity and water-holding capacity of soil.

In mosses, the sporophyte is a much more distinct phase of the life cycle than is the case with liverworts, although it is dependent

* Many species of algae and fungi have dimorphic life cycles.

† You might find it helpful at this point to read the discussion on reproduction in mosses and ferns (this is Section 8.4). A few terms there will be unfamiliar, but the material should prove helpful in understanding dimorphic life cycles at this point.

upon the gametophyte throughout its existence. Typically, it is a stalk borne at the top of a gametophytic plant, and features a structure (*sporangium*) located at the tip, where spores are produced (Figure 4.33).

Ferns and fernlike plants Thus far, we have considered plants which are, in general, rather small. This is a reflection of their lack of structural complexity, especially the absence of specialized tissues for the conduction of water. The land plants, particularly, cannot grow to a very great size because there is a mechanical limit to the distance water can travel from cell to cell.

In contrast, the ferns (Figure 4.34) exhibit a degree of structural complexity that far exceeds any of the plants we have considered thus far. This is chiefly because they possess specialized tissues which conduct fluids throughout the plant body. These are called *vascular tissues*, and those plants which possess them (ferns, fernlike plants, and seed plants) are called *vascular plants*. There are two types of vascular tissues, *xylem* and *phloem*. In general, xylem tissues conduct water and dissolved minerals from the root upward, and phloem tissues transport newly manufactured food materials downward from the leaves. Phloem also transports storage materials upward in plants which live for several years and which begin a growing season by utilizing foods stored in the stem or roots. Some representative vascular tissues of higher plants are shown in Figure 4.35.

The ferns themselves usually do not attain great size, although the tree ferns of the tropics may reach a height of 80 feet, and it is known that species which are now extinct were much larger than any present-day ferns. In common species of the temperate zone, the



Figure 4.34 Typical ferns of the temperate zone as seen on the forest floor. (U.S. Forest Service.)

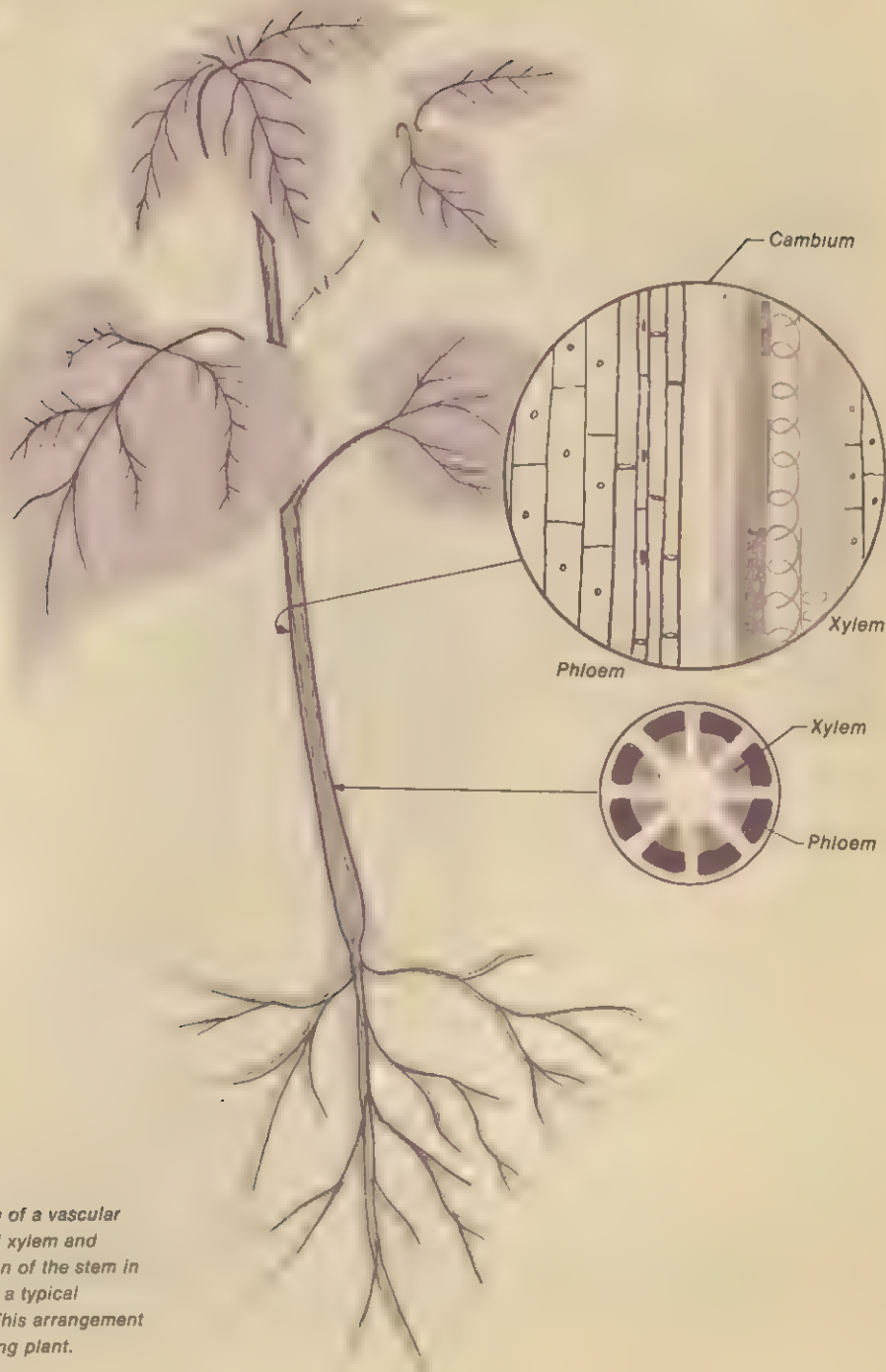


Figure 4.35 Generalized drawing of a vascular plant, showing the arrangement of xylem and phloem tissues. Top inset, a portion of the stem in longitudinal section; bottom inset, a typical cross-sectional view of the stem. This arrangement is that of a dicotyledonous flowering plant.

sporophytic plant exhibits a subterranean stem called a *rhizome*, from which roots project in a positive response to gravity and from which leaves, called *fronds*, extend upward. Almost all species are perennial, that is, the rhizome and roots live for many seasons, and new fronds are produced every year.

You will recall that in liverworts and mosses the gametophyte is more prominent than the sporophyte. This situation is reversed in ferns, where the sporophyte is far larger and more complex than the gametophyte. The fern plant itself, consisting of roots, rhizome, and fronds is the sporophyte. The gametophyte is a very small plant, generally less than a quarter-inch in diameter, from which the sporophyte develops.

Ferns are not of great economic importance to man, although some of the larger ferns are grown for ornamental purposes. About 300 million years ago, however, ferns and fernlike plants constituted the bulk of the vegetation on earth. Conditions were such that great masses of these plants were preserved, and their bodies were slowly transformed to coal. In this respect, ferns of the past have provided a fuel substance which is of considerable economic importance to man.

Seed plants Some 300 million years ago, while ferns were at their peak, a new structure for plant reproduction appeared. Apparently, it developed first in certain ferns, called seed ferns, which are now extinct. Although modern ferns do not bear seeds, there arose a distinct plant group from the seed ferns which gradually replaced ferns as the major vegetation on earth. These are the seed plants, and they are presently the most numerous plants in nature. Well over 200,000 species of seed plants have been classified, which means that they outnumber all other plants combined. Species vary in size and form all the way from extremely small plants to giant trees, and as a group they occupy virtually all types of habitats.

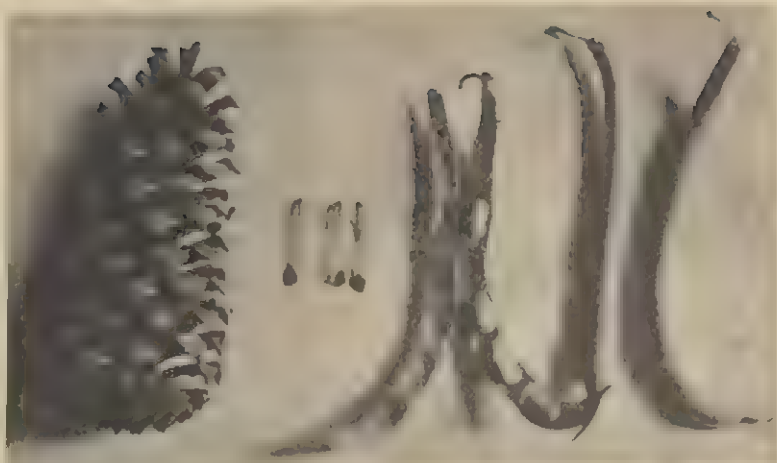
In seed plants, the gametophyte is quite reduced in size relative to that of the sporophyte. In fact, the sporophyte is the plant body itself, and the male and female gametophytes are microscopic in size. Furthermore, they have no independent existence apart from the sporophyte. Reproductive events are such that an embryonic sporophyte is produced within reproductive tissues, and after it develops to a certain point, it stops growing and becomes dormant. At this stage it is still a very immature plant, and in most species, it is extremely small. Tissues developed in association with the growth of the embryonic sporophyte surround it with storage materials and protective coats, so that a seed is actually a young sporophytic plant plus these associated structures. As the seed itself matures, it is shed from the plant, and may eventually germinate to produce a mature sporophyte under proper environmental conditions.

Figure 4.36 A stand of young pine trees, showing typical slender growth of trunks.



The seed plants may be conveniently divided into two groups on the basis of their reproductive structures. One group, the *gymnosperms* (Gr. *gymnos*, naked + *sperma*, seed), bear seeds which usually are exposed on the plant. Although several types of gymnosperms are recognized, the *conifers* represent the largest group. These are trees or shrubs which bear their seeds upon scales within structures called cones. The vast majority, of which pine (Figure 4.36), fir, and spruce are representative, are *evergreens*, but a few species such as larch and bald cypress are *deciduous*. Many species of conifers assume considerable importance as a source of wood and other products. In contrast to the gymnosperms, the *angiosperms* (Gr. *angeion*, vessel + *sperma*), or *flowering plants*, bear seeds enclosed within a structure which arises from a part of the flower (Figure 4.37). Within the seed plant group, the angiosperms are by far more successful and numerous than the gymnosperms. The latter number less than one thousand species, whereas there are at least 200,000 known species of flowering plants. Hence, they are more numerous than all other plants combined, which explains why most plants encountered in nature belong to this group. Virtually all species

Figure 4.37 A contrast between the seed-bearing habits of gymnosperms and angiosperms. The seeds of pine, which are winged, are borne upon the scales of the cones, which open and release the seeds. The bean pods are ripened ovaries of flowers, and the seeds are borne within them



cultivated by man are flowering plants, as are all trees except gymnospermous species.

The structure common to all species of angiosperms, the flower, is a plant organ whose function is the formation of seeds in reproduction. There is a considerable variety in flower form, the typical structure being a showy, symmetrical aggregation of spore-bearing and sterile parts. Many flowers, however, such as those of grasses, do not exhibit such prominence.

The flowering plants usually are divided into two groups, the *monocotyledons* and *dicotyledons*, which are names describing embryonic structure in the respective groups. A *cotyledon* may be described as a seed leaf of the embryonic sporophyte; monocotyle-

Figure 4.38 Contrast of corn seed (monocotyledonous) with castor bean seed (dicotyledonous). Each sectioned seed is drawn in such a manner as to show the embryonic sporophytic plant in each case.

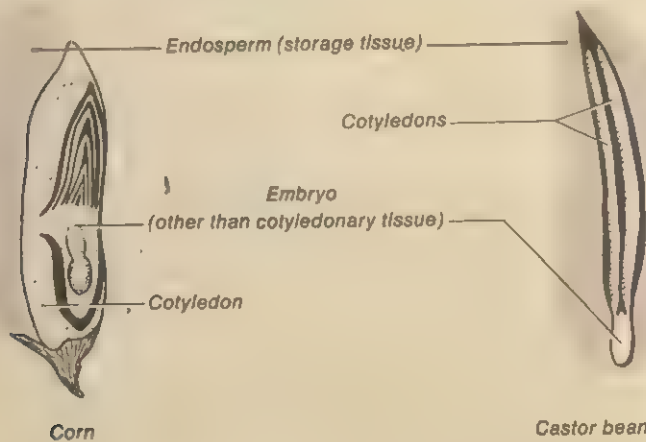




Figure 4.39 An experimental field of corn, which is monocotyledonous. Note slender leaves with parallel veins, which is typical of this plant group. (Allied Chemical Corporation.)



Figure 4.40 A bean plant, showing the broad leaves and netted arrangement of veins characteristic of dicotyledonous plants. Note the two shrivelled cotyledons still attached to the stem; in beans, these structures are carried above ground by the emerging shoot and eventually fall off.

donous plants possess one such structure, whereas dicotyledonous plants have two (Figure 4.38). In general, the monocotyledons are plants whose leaves are slender with veins running parallel to each other, such as grasses, cereal grains, and certain ornamental plants (Figure 4.39). The dicotyledons usually bear leaves which are broader and whose veins are not parallel; cotton, beans, and oak trees exemplify dicotyledons (Figure 4.40).

The seed plants, and especially the angiosperms, are of more economic importance to man than all other plants combined. The larger trees, such as pine, oak, and hickory, are sources of lumber and a variety of wood products. The fibers of cotton, flax, jute, and many other plants are important to the textile industry. Some flowering plants, such as poppies and the cinchona tree, are sources of drugs, and the coconut palm and olive tree are representative of those plants from which valuable oils are obtained. Almost all edible plant products are obtained from seed plants. Cereal grains, such as wheat and rice, have been cultivated for thousands of years. Many



Figure 4.41 Graphic representation of the accumulation principle with regard to several important features of plants. Open squares mean "characteristic lacking," shaded squares mean "characteristic present," partially shaded squares mean "characteristic present in some species."

other plants have been developed for their fruits, among which are apples, bananas, citrus fruits, and so on. The list could be extended very far indeed. The roots, stems, and leaves of many flowering plants are edible; representative of these three plant structures, respectively, are sweet potatoes, sugar cane, and cabbage. This list is hardly a complete one, but it does indicate the tremendous economic importance of the seed plants.

Although "accumulation" of adaptations is perhaps less obvious among plants than is the case in the animal kingdom, we can trace a few important structural advances from the simplest plants to those that are most complex (Figure 4.41). This indicates a certain kinship

among plants, just as with animals, and we shall see later on that there are other evidences which tend to verify this principle.

We have devoted some attention in this chapter to the major plant and animal forms which inhabit the earth at the present time. Our rationale for considering plant and animal diversity at this particular point in the book is that of providing a sense of orientation before studying major characteristics of living forms. Somewhat secondary, but nevertheless important, is the fact that a well-educated person should be aware of and generally familiar with the living forms which he observes about him, and with some of the methods which professional biologists employ in studying organisms.

4.5 Summary Biologists approach the problems of taxonomy through a modern application of the system devised by Carolus Linnæus in the eighteenth century. According to the modern viewpoint, classification should reflect the evolution of plant and animal groups as nearly as evidence allows.

Our survey of the animal kingdom takes into consideration ten major animal phyla, many of which include several important classes. As we have listed them, these phyla are the Protozoa, Porifera, Cnidaria, Platyhelminthes, Nematoda, Mollusca, Annelida, Arthropoda, Echinodermata, and Chordata. They include some 99 percent of the known animal species.

We have made no attempt to present the plant kingdom in terms of formal phyla or divisions; rather, we recognize seven groups of plants. These are the algae, the fungi, the lichens, the liverworts, the mosses, the ferns and their allies, and the seed plants. Several subgroups are discussed, especially those of the algae, the fungi, and the seed plants.

- Questions**
- 1 What is the difference between natural and artificial approaches to classification?
 - 2 Write an improvement of this poor definition: a species is a group of similar organisms.
 - 3 What do your authors mean by saying that at the species level of classification, terminology must bridge the abstract and the concrete?
 - 4 Contrast the two-kingdom and four-kingdom approaches to classification. What does each approach have to recommend it?
 - 5 There are more known species of insects than of all other animals combined. Can you advance any possible explanation for this?

6 To what extent is radial symmetry an indicator of relative simplicity? In view of the fact that virtually all animals except those which are quite low in the phylogenetic scale exhibit bilateral symmetry, why are echinoderms placed as high as they are?

7 Explain this statement: all vertebrates are chordates, but not all chordates are vertebrates.

8 Does the accumulation principle as applied to the animal kingdom mean that evolution proceeded from the Protozoa to the Chordata one phylum at a time? How else might it be interpreted so as to be a meaningful concept?

9 Mechanically speaking, what advantages does an exoskeleton have over an endoskeleton, and vice versa?

10 Contrast the respective roles of algae and fungi in nature. How are these roles related to their nutritional habits?

11 In what respect are lichens unusual plants?

12 Generally speaking, vascular plants reach much larger size than do nonvascular plants. What possible explanation can you give for this?

13 There are more known species of flowering plants than of all other plants combined. Can you advance any possible explanation for this?

14 Consider the following terms, selected at random from the material of this chapter. Without defining them precisely, tell how each is significant to an understanding of the world of life: notochord, heterotroph, alternation of generations, tube-within-a-tube, seed, xylem, chitin, chlorophyll, flower, metazoa, evolution, protista

15 The authors of a biology textbook state in their introduction, "We maintain that a person is infinitely better off if he knows something of the plants and animals in his surroundings. To walk among the sights and sounds of nature without awareness is little short of tragic." Is this a sufficient rationale for studying biology? In what other ways might a study of plants and animals be beneficial to a person who seeks to be liberally educated?

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Regulation and control in living systems

If we had to select a single key word that best describes what we have learned so far about living systems, it would be the word "complexity." In fact it is difficult to justify the use of the contrasting term, "simplicity," at any level of organization, except in a purely relative sense. Because living systems are complex, biologists face many unsolved problems, some of which are basic to an understanding of the phenomenon we call life.

One of the most fascinating problems in biology is that of regulation and control. For years, we have been asking such questions as these: How does a cell maintain a balance of materials within its boundaries? How does it "turn on" and "turn off" the production of certain key substances? How are cellular activities coordinated in the organism so that it maintains balance as a whole? What is the mechanistic basis of genetic action in living systems at all levels? Is there a balance of organisms in nature? We shall not answer these and similar questions in this book; some are as yet unapproachable, others are incompletely understood, and still others involve levels of sophistication beyond the scope of this book. Nevertheless, we shall attempt to set forth some of the basic factors involved in regulation and control, and these factors will provide some basis for understanding the characteristics of metabolism, growth, reproduction, responsiveness, and adaptation, which are discussed subsequently in separate chapters.

5.1 The steady state

As long as a living system is able to maintain itself by coordinating its several activities, it is said to be in a *steady state*. This is accomplished at all levels by *homeostatic mechanisms*, or, as they are sometimes called, *steady-state controls*. The complexity of living systems is such that these controls are not always readily apparent; we are obliged to assume their existence in some cases, although many are known at various levels of organization. The concept of homeostasis is of sufficient importance that we might even formulate a definition of life in its terms. As long as a system maintains homeostasis, it is alive; when any of its controls get irreparably out of balance, it dies. This inevitably happens because a perpetual balance of controls is impossible.

Presently, we shall investigate some homeostatic mechanisms at three levels of organization, but first, let us consider a mechanical analogy to homeostasis. Of course, inanimate systems do not compare in complexity with living systems, but the very simplicity of our example should serve to illustrate the principle which we seek to clarify.

The *thermostat* is a very simple device (compared with steady-state mechanisms of living systems) that regulates temperature. In its most rudimentary form, a thermostat consists of a temperature-

sensitive metallic strip which makes or breaks an electrical contact. Let us suppose that it is regulated to make contact at 71 degrees Fahrenheit and break it at 73 degrees. Mechanically, this is rather easily arranged by a simple spring mechanism. If the temperature of a room falls to 71 degrees, the metal strip makes contact with a wire which is so arranged that an electrical circuit is established. Upon contact, the current "comes on" and starts a furnace. The heat thus supplied affects the thermostat, and since it breaks the circuit at 73 degrees, the furnace shuts off at that temperature. Thus, the whole system is homeostatic, or self-regulating (Figure 5.1), and the temperature of the room is maintained at a steady state (if a range of two degrees is considered steady by the occupants of the room).

In applying the concept of homeostasis to living systems, we must understand that even the simplest mechanisms are vastly more complex than the thermostat, which we present more as an analogy than as an example. Furthermore, not all regulatory and control mechanisms are homeostatic *within themselves*. Although we can find numerous examples of *apparently* self-regulatory mechanisms, they are almost always influenced by other factors within the living

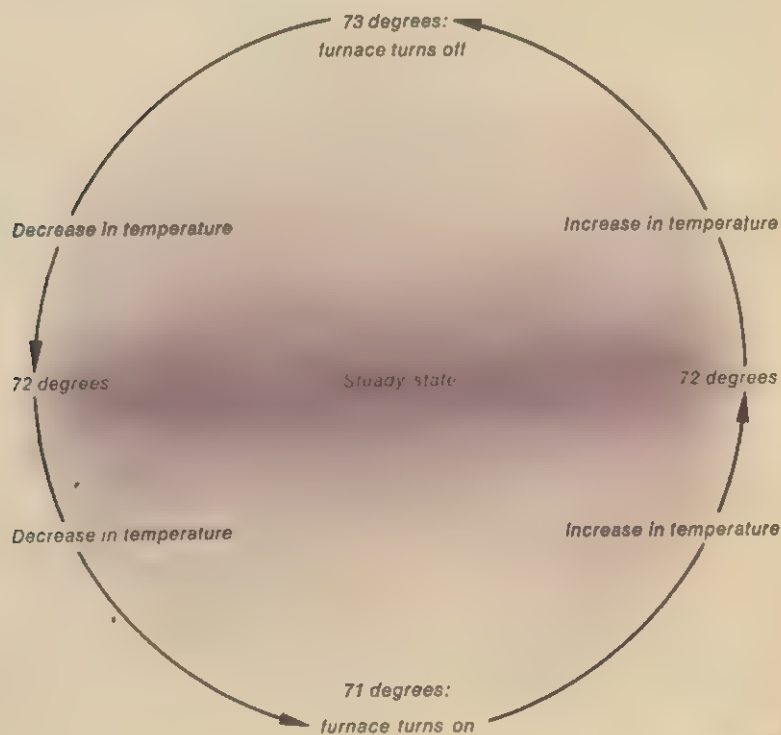


Figure 5.1 Diagrammatic representation of steady-state temperature as it is regulated by a thermostat. The temperature is "steadiest" at 72 degrees Fahrenheit.

system. In addition, some mechanisms of regulation and control are homeostatic only in the sense that they contribute to the steady state of an entire cell, organism, or group of organisms. As a matter of fact, a living system is anything but steady in its operation. All sorts of factors are in a constant state of flux, and what we call a steady state is actually a dynamic equilibrium brought about by the coordination of many controlling mechanisms. In an absolute sense, a system is steady only when dead, even then its decay is unsteady.

Regulation and control at the cellular level 5.2 To a great extent, regulation and control within a cell are the result of interaction between nucleus and cytoplasm. Strictly speaking, not all these mechanisms are homeostatic within themselves; in fact, as we shall see, the steady state of a cell (or of an organism) is maintained by the interaction of many separate controls, and we need not expect every mechanism to correspond to our simplified example of a thermostat. Thus the complex interactions between nucleus and cytoplasm frequently defy any immediate identification with the steady state; and in the main we shall attempt to describe only important mechanisms in these areas of the cell.

The role of the nucleus Because the nucleus usually occupies a central location in the cell, it has long been suspected of governing the remainder of the cell. This hypothesis was strengthened in the latter part of the nineteenth century, when it was discovered that the nucleus exhibits a complicated pattern of events in its division during cell reproduction; the precision with which chromosomes apparently divided seemed to indicate a high degree of organization in the nucleus. Thus it was concluded that the nucleus probably contained the machinery for controlling cellular activity, even though techniques were not available for testing this hypothesis. However, in 1928 the embryologist Hans Spemann conducted an experiment which indicated something of the role of the nucleus in development. Working with fertilized eggs of a salamander, he used a fine hair to hasten constriction at the first cleavage.* He drew the hair tightly before the nucleus had divided, so that one daughter cell included the nucleus while the other consisted only of cytoplasm. Spemann did not separate the two cells completely, but only sufficiently to prevent the passage of a nucleus from one cell to the other. Under these conditions, the cell with nuclear material continued to divide, but the cell without nuclear material remained undivided. However, after about sixteen cells had been produced by the original nucleated cell, the nuclei became much smaller, and a single nucleus

* It will be helpful to read Section 7.2 on cell division at this point.

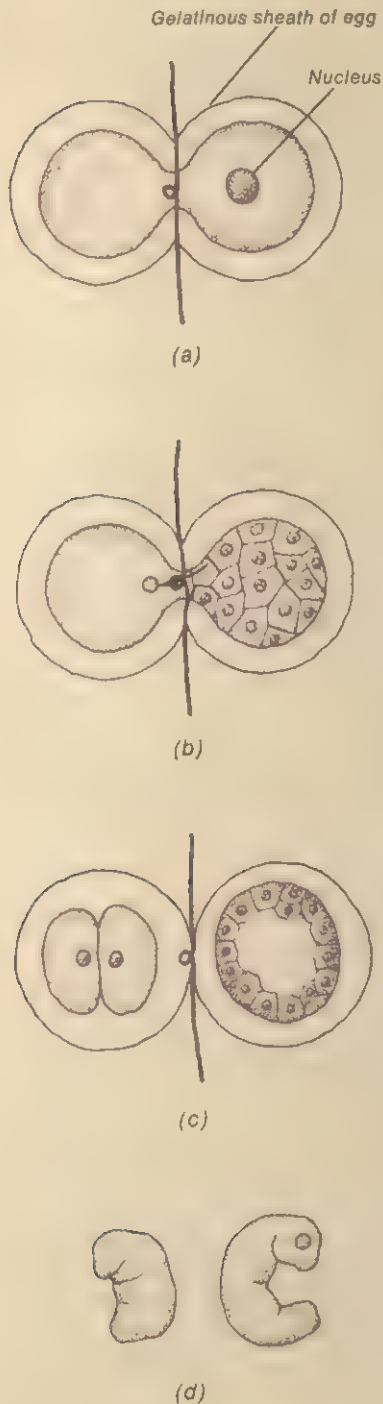


Figure 5.2 A series of diagrams showing Spemann's experiment with salamander embryos. (a) The fertilized egg is constricted by a thread so that one half contains no nucleus. (b) Cleavage occurs in the nucleated half until sixteen cells are formed; no cleavage occurs in the half without a nucleus. At this point, a nucleus is allowed to pass from one side to the other. (c) Cleavage begins in the left-hand half; the right-hand half is now well advanced. (d) Both halves form normal embryos, although that derived from the left-hand half is not so advanced as that from the right-hand half at the stage shown.

was allowed to pass into the undivided cell. At this point, Spemann separated the two cell groups by drawing the hair tightly, and the undivided cell began to divide (Figure 5.2). Subsequently, a normal salamander embryo developed on each side of the hair constriction. This work indicated strongly that the nucleus exerts a vital control upon cell division and embryonic development.

More recently, methods have been developed whereby nuclei may be removed from cells without damage either to the cells or to the nuclei, and two lines of work are significant to our discussion. The first type of experiment has been carried out using *Amoeba*, where nuclei were removed by means of delicate surgical instruments. Such cells, devoid of nuclei, are capable of living for several days. However, they never reproduce, and they eventually lose their homeostatic balance and die. It is significant that a nucleus can be taken from another amoeba and transplanted to one of the cells which has been deprived of its nucleus; if disorganization has not proceeded too far, this cell will then recover and go about its activities in a completely normal fashion (Figure 5.3).

The second line of work which is relevant to our discussion at this point is that of the German cytologist J. Hammerling in the 1950's on the green alga *Acetabularia*. This is a rather unusual organism; although it is unicellular, it reaches a height of 2 inches, and at maturity it consists of a well-differentiated stalk and cap (Figure 5.4). The nucleus resides at the base of the stalk. It occurred to Hammerling that if the nucleus influences development in this plant, it must do so by a form of remote control, since the cap is located some 2 inches from the nucleus. This organism is highly regenerative; if a cap is removed from the rest of the cell, a new cap is regenerated.

In one series of experiments, Hammerling used two species of *Acetabularia*, *A. mediterranea* and *A. crenulata*, which differ in cap shape. In both species, he found that if a piece of stalk is removed from the region between the cap and its nucleus, it will commence regeneration, but will not develop very far before it dies. This, of course, is what we would expect on the basis of earlier work involving the role of the nucleus. Hammerling undertook some grafting experiments in order to determine the influence of the nucleus upon

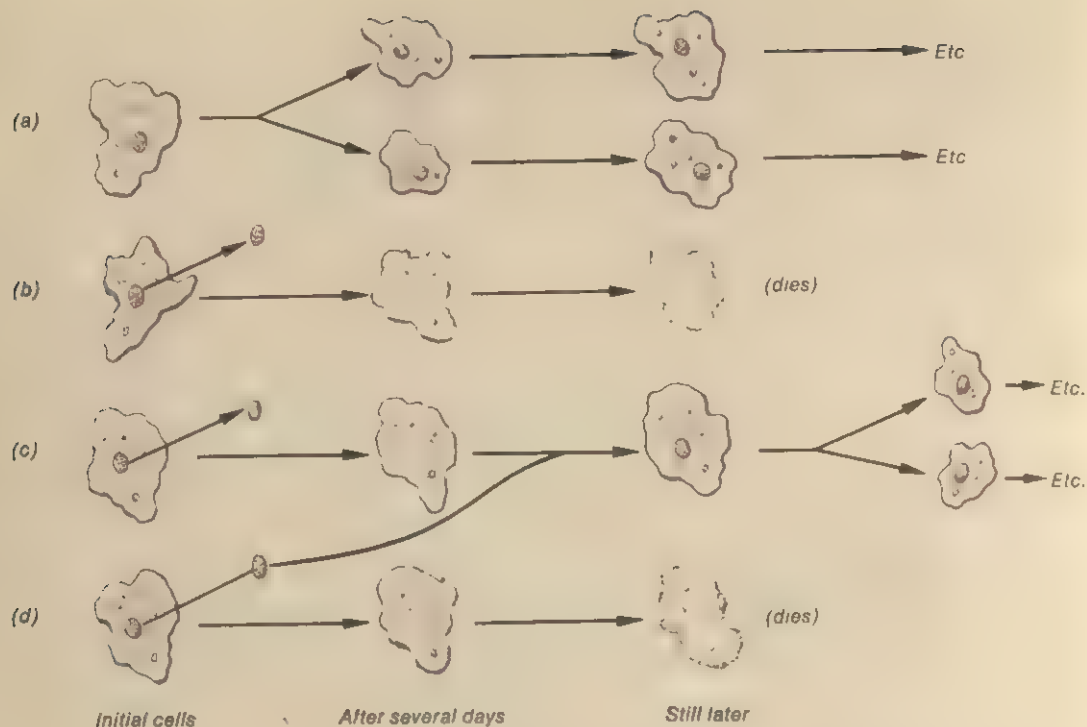
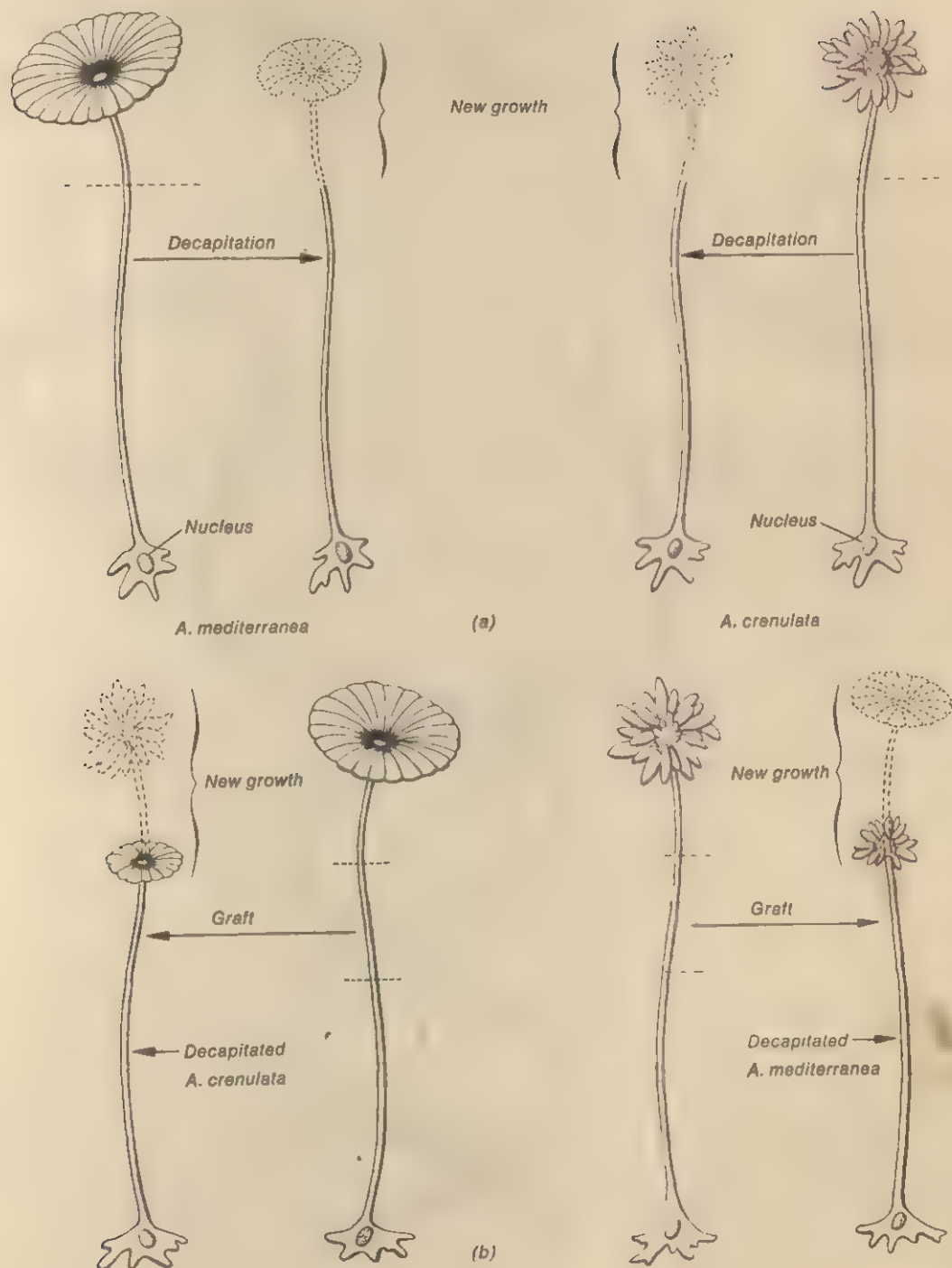


Figure 5.3 A series of diagrams showing transplantation experiments with *Amoeba*. (a) Normal divisional pattern of *Amoeba*. (b) Removal of nucleus results in ultimate death of cell. (c, d) Nuclear transplant rejuvenates enucleated cell; donor cell dies.

cap formation, and his results were most significant. He grafted a piece of *A. mediterranea* to a decapitated *A. crenulata*, and vice versa; in each case, the cap started forming in the shape it would normally have assumed, but eventually, it changed over and assumed the shape characteristic of the base which contained the nucleus. These experiments are also shown in Figure 5.4. Apparently, the cytoplasm contains substances which bring about developmental changes, but the nucleus dictates the formation of these cytoplasmic substances. This would account for the delayed action

Figure 5.4 Experiments involving the green alga *Acetabularia*. (a) Decapitation and subsequent regeneration of cap is specific for each species. (b) Grafting experiment. If a piece of stalk from *A. mediterranea* is grafted to a decapitated *A. crenulata*, regeneration begins with the formation of a cap characteristic of *A. mediterranea*. However, the cap ultimately assumes the shape characteristic of the piece (base) containing the nucleus (*A. crenulata*). The reciprocal experiment (shown at right) yields similar results.



in the grafting experiments; it would seem that as long as the cytoplasmic substances are present in the grafted piece, initially formed under the influence of the original nucleus, development proceeds as it would have done had the piece never been removed from its

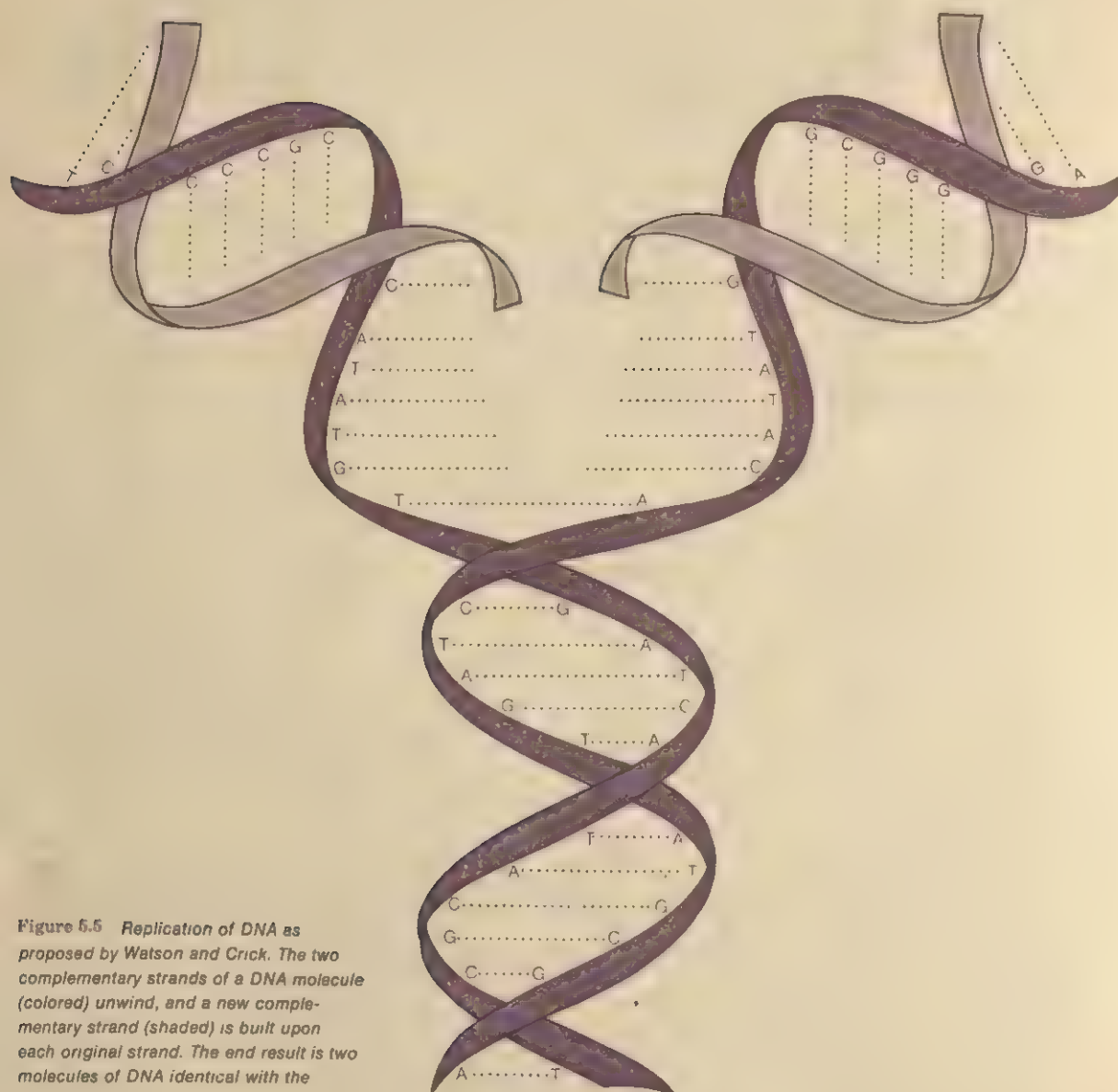


Figure 6.5 Replication of DNA as proposed by Watson and Crick. The two complementary strands of a DNA molecule (colored) unwind, and a new complementary strand (shaded) is built upon each original strand. The end result is two molecules of DNA identical with the original.

nucleus. However, as soon as these substances are used up, they are replaced by other substances which are formed under the influence of the new nucleus.

Nuclear cytoplasm control During the late 1940's and the 1950's, significant discoveries regarding the role of the nucleus followed each other in rapid-fire order. This area became a lively one in research; biochemistry, biophysics, cytology, embryology, and genetics all became involved. Many cell organelles other than the nucleus, particularly ribosomes, were studied in conjunction with the nucleus, and the proteins and nucleic acids received close attention. We shall make no attempt to trace the sequence of events historically, but rather, the account which follows is a summary of present knowledge with regard to some of the more significant factors involved in nuclear control and regulation.

The chromatin material of the nucleus is composed largely of DNA and protein. Many lines of evidence implicate DNA as the control material of the nucleus, that is, it serves as a kind of "code" which "instructs" the cytoplasm in a highly specific manner. According to the Watson-Crick model of DNA (Figure 2.25), this substance consists of two helical strands of sugar-phosphate molecules between which four kinds of nitrogenous bases are linked together in pairs. Apparently, a DNA molecule is replicated (reproduced) whenever the weak hydrogen bonds between linked base pairs break, the two complementary strands unwind, and a new strand is built up on each original strand from micromolecular components present in the nucleus (Figure 5.5). Each new double-stranded molecule then assumes the characteristic helical form. On occasion, however, one (but apparently not both) of the two DNA strands may "template" a complementary strand of RNA, not DNA. Whenever this occurs, the base *uracil* is used as a "substitute" for the base *thymine*. In other words (as we noted in Section 2.4) the four nitrogenous bases found in DNA are adenine, cytosine, guanine and thymine, but the four found in RNA are adenine, cytosine, guanine and uracil. Whenever RNA is synthesized in this fashion, it does not remain joined to its complementary DNA strand; rather, it moves away, and the DNA strand may serve as a code, or template, for the assembly of another strand of RNA. By using the first letters of the five different bases involved in DNA replication and RNA synthesis, let us compare these processes in a short segment of a hypothetical DNA molecule (Figure 5.6). You will note that DNA and RNA are differentiated by color, and we shall follow this pattern as we present subsequent diagrams. Note that the synthesized RNA molecule is single-stranded, in contrast to the double nature of the DNA molecule. Furthermore, it appears that RNA molecules are produced in

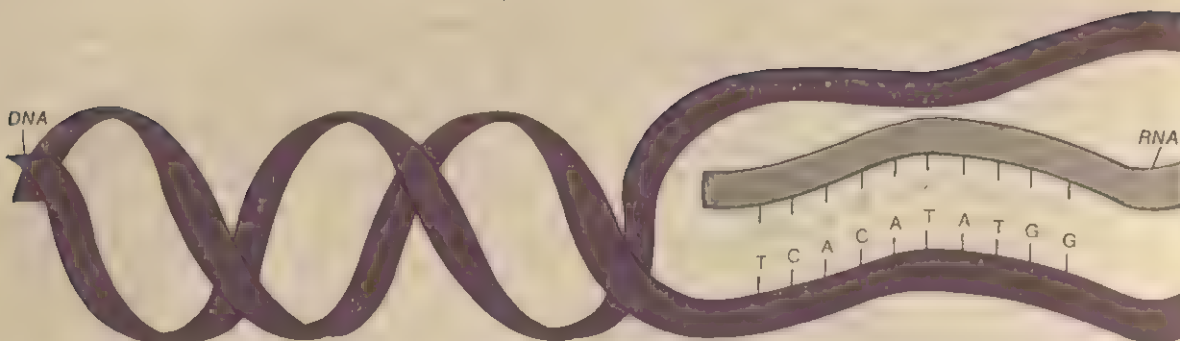


Figure 5.6 RNA synthesis on one strand of a DNA molecule, greatly simplified. Notice that uracil, not thymine, is coded by adenine

shorter segments than the entire DNA strand from which they are templated. However, they are ordinarily much longer than the segment shown in Figure 5.6, which we have oversimplified for illustrative purposes.

What happens to the RNA molecules thus formed? It appears that they pass out of the nucleus into the cytoplasm, where they eventually carry the code to the ribosomes. For this reason, this particular kind of RNA is called *messenger RNA* (abbreviated *mRNA*). The RNA which composes ribosomes is called *ribosomal RNA* (*rRNA*) and it is apparently formed in a somewhat different fashion from *mRNA*.* Upon reaching a ribosome a given *mRNA* molecule attaches in some manner to its surface or to the surface of an aggregate of ribosomes. The *mRNA* code, consisting of a specific base sequence, is exposed as an outer surface (Figure 5.7). Meanwhile, still another kind of RNA is active in the cytoplasm. It is called *transfer RNA* (abbreviated *tRNA*, or sometimes *sRNA*, for *soluble*), and its individual molecules are much smaller than either those of *mRNA* or ribosomal RNA, in each molecule of *tRNA*, a chain of about seventy nucleotides is folded so that it resembles a short DNA molecule (in that it is a double-stranded helix). Apparently, the region of the "bend" of the *tRNA* molecule is specific as a point of attachment to *mRNA*, and one of the open ends is specific as a point of attachment to an amino acid. For example, a certain type of *tRNA* will attach only to the coded "alanine site" on a given *mRNA* molecule (Figure 5.7). It appears that *tRNA* molecules are the same in all kinds of cells, thus, we can visualize twenty different kinds of *tRNA* molecules to correspond

* Some investigators believe that *rRNA* is merely *mRNA* which has become incorporated into the ribosome. For our purposes, we shall consider that they are separate entities.

with the twenty different amino acids ordinarily involved in protein synthesis. Attachment of an amino acid to a given tRNA molecule is accomplished enzymatically, and is accompanied by the expenditure of energy on the part of the cell.

Many lines of evidence indicate that three mRNA nucleotides are required to code an amino acid. Thus, if a molecule of mRNA consists of thirty nucleotides, as we have shown in our accompanying drawings, ten molecules of tRNA can be accommodated, each of which carries an amino acid to the messenger RNA-ribosomal complex (remember, our numbers are greatly reduced for purposes of illustration). Eventually, the specified kinds of tRNA, each with an

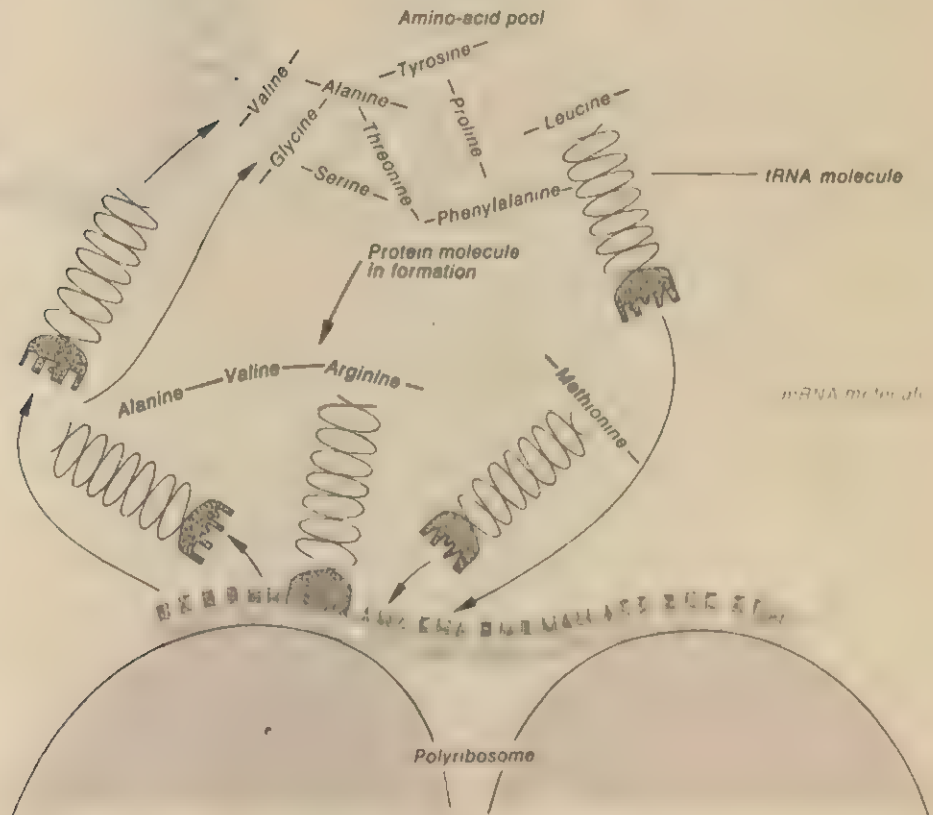


Figure 5.7 A model showing the synthesis of protein. Specific tRNA molecules pass successively along the mRNA molecule and each contributes its amino acid molecule to the developing protein molecule. The tRNA molecules then return to an amino acid pool for another "load." Notice that a triplet of mRNA nucleotides codes a single amino acid.

amino acid in tow, attach at specific sites on the mRNA molecule. These amino acids are joined enzymatically by peptide linkages, and a protein molecule is thus formed (Figure 5.7). The protein molecule breaks away and becomes functional as an enzyme or as a structural protein, and the ten molecules of tRNA are released from the mRNA molecule, at which point they return to the general cytoplasm for another load. In contrast, there is a very rapid turnover rate of mRNA molecules, at least in bacterial cells, where it appears that a given molecule of mRNA may code only a single protein. After this, it is broken up and replaced by another mRNA molecule. However, it is probable that in some protoplasmic systems mRNA is longer-lived.

Now let us return to a consideration of the role played by DNA in cellular control. It is obvious that the *ultimate* template for protein synthesis is the DNA molecule, and it is in this role that DNA exerts its effects upon the remainder of the cell. As a matter of fact, it appears that the nucleus controls the cytoplasm *only* through this channel. Protein molecules are so diverse within living systems that their expression within cells (mostly as enzyme molecules) ultimately accounts for most of the activity of living systems at all levels of organization.

Perhaps an analogy will serve to clarify the DNA-RNA-protein synthesis sequence we have outlined above. Let us suppose a certain library possesses a copy of a rare old book, perhaps a Gutenberg Bible. Certainly, the library is not going to lend this book, inasmuch as it might easily be lost or damaged. However, it might allow the book to be photographed page by page so that facsimile copies could be made. These copies might then be used in private studies for the preparation of scholarly papers, which in turn stimulate learned activity. DNA is something like the rare book. It never leaves the nucleus, but instead, copies in the form of mRNA are released to the cytoplasm. Finally, proteins are formed, and they become directly involved in cellular activity.

Now we are in a much better position to understand the nuclear transplant work discussed above. In *Acetabularia*, for example, it seems probable that a grafted stalk piece contains a certain quantity of mRNA and protein formed under the influence of the original nucleus. Thus, development of a cap proceeds in the direction which would have been taken had the stalk remained under the influence of the original nucleus. However, before development proceeds very far, new mRNA (from a different nucleus) replaces the old mRNA, and new proteins take over the developmental process. As a result, the cap which eventually forms is characteristic of the species which receives the graft, not of the species from which the stalk was taken.

Again, let us consider the matter of cell size. As we learned in

Chapter 3, there is an apparent limit to the amount of cytoplasm which can be controlled by a single nucleus. This is indicated by the fact that when cells reach a characteristic size, they divide. Furthermore, exceptionally large cells, such as those of certain protozoa, may contain a nucleus in which the DNA content has multiplied in some fashion. In *Acetabularia*, which is an unusually large cell, the nucleus is actually a composite of many small nuclei, and it appears that the amount of DNA is thus increased to a point at which control is possible. Although other factors may limit cell size (for example, the surface area-volume ratio), the nuclear-cytoplasmic ratio is apparently a critical factor in this regard. At the lower limits, in turn, a cell would have to be large enough to contain a minimum number of the macromolecules which constitute the cellular machinery. Several lines of evidence suggest that a cell could hardly be less than $0.05\ \mu$ in diameter and contain the minimum number of molecules; the smallest cells known, the pleuropneumonia-like organisms, are about $0.1\ \mu$ in diameter.

The regulation of protein synthesis Perhaps our discussion of nuclear control, presented above, has conveyed the impression that the protoplasmic mechanisms involved are relatively simple. This would be an unfortunate impression, because even this one aspect of control is fantastically complex. As is so frequently true in science, the answer to one question may breed a dozen new questions, and this has occurred with regard to protein synthesis. For example, assuming that we have answered the question of *control* in cells (and this is most certainly an assumption—we have hardly done more than approach the problem), how is protein synthesis *regulated*? This question is an urgent one, especially in view of the fact that numerous kinds of mature cells of an organism are so variously specialized in their functions. For instance, how is it that a human liver cell differs in its chemical activities from a muscle cell? How did each cell become what it is? If the DNA content of each cell is identical, why are the same proteins not produced by way of the DNA-RNA-ribosome pathway, or if they are, why do they not govern activity in similar fashion within different cells? One possible approach to answering these questions would be to investigate cytoplasmic differences, and we shall examine this possibility in Chapter 7. But first, let us seek some tentative answers within the framework of the present topic.

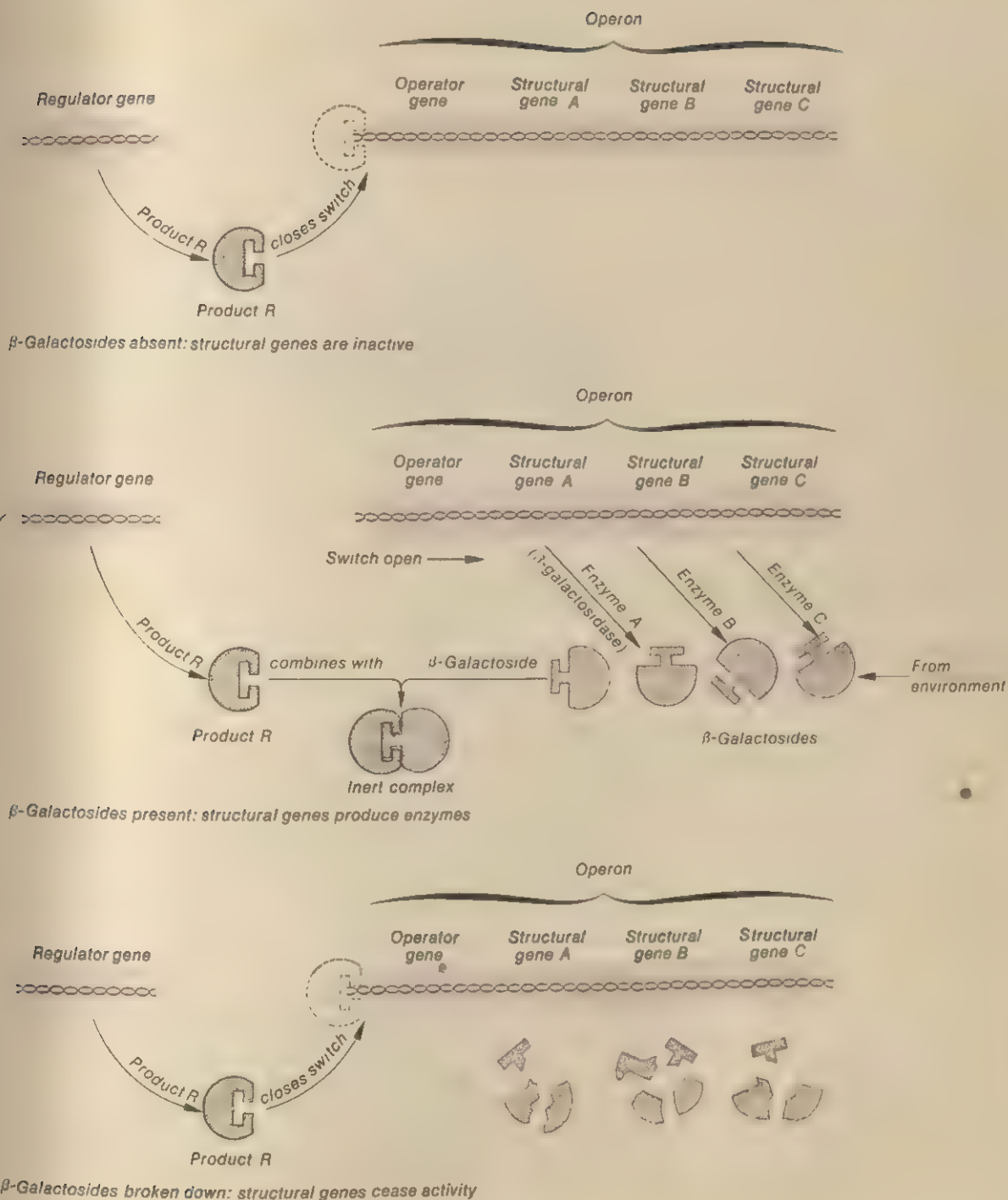
In 1961, two French biologists, François Jacob and Jacques Monod, proposed a model of cellular regulation based on their work with microorganisms. Although it is still too early to assess the value of this model as a working theory at all levels of organization, it constitutes the most attractive hypothesis yet proposed for the

pursuit of further experiments in cellular regulation. Jacob and Monod found that the concentration of certain proteins fluctuates greatly in some strains of bacteria, depending upon the nutritive environment. For example, the bacterium *Escherichia coli* is able to utilize a group of carbohydrates called the β -galactosides by attacking them with an enzyme, β -galactosidase. Analysis reveals that when β -galactosides are absent from the medium (*E. coli* may utilize other carbohydrates), no β -galactosidase is present. Only when the substrate is present does the bacterium produce the appropriate enzyme. This is typical of a whole class of enzymes, of which β -galactosidase is only one; still other enzymes are always produced, whether their substrate is present or not.

Based on this and other evidence, Jacob and Monod proposed a unit of genes called an *operon* which is postulated to work in conjunction with a *regulator* gene. Just here, we must point out that we are using the term *gene* to correspond to a given segment of a DNA molecule which codes a segment of mRNA, which in turn codes a protein molecule. At least, this is *one* kind of gene, and to distinguish it from other types, we shall call such a segment of DNA a *structural* gene. According to the Jacob-Monod model, two other kinds of genes exist, at least functionally. These are known as *regulator* and *operator* genes, respectively; it appears that these two types of genes do not govern the ultimate formation of metabolic enzymes, but rather, they code for substances (probably proteins) which exert their effects within the operon system.

Now let us see how the system works. Let us assume that the operon consists of four genes: the operator gene and three structural genes, A, B and C (Figure 5.8). Gene A represents the DNA segment responsible for the production of β -galactosidase, and B and C represent genes which code for associated enzyme molecules with which we will not be concerned at this point. The operator gene acts as a switch; when it is open, the structural genes are active, and when it is closed, the structural genes are inhibited. The operator remains inoperative (closed) as long as a repressor substance, produced by the regulator gene, is present. Whenever β -galactoside is present in the environment, however, it reacts with the repressor substance and "binds" it so that it is no longer capable of repressing the operator gene. At this point, the operator switches on, and the

Figure 5.8 A model of gene regulation and control according to the operon concept of Jacob and Monod. The regulator gene controls the action of the operator gene as long as no substrate is present, thus inhibiting the production of structural enzymes A, B, and C. When a substrate is present, it ties up product R, thus allowing the operator gene to "switch on" the structural genes under its control.



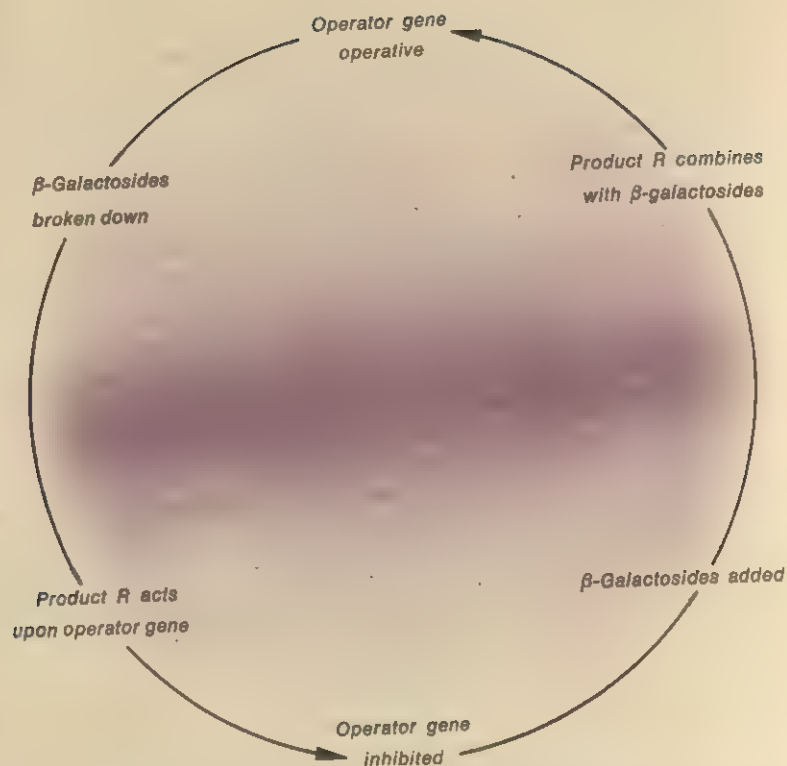


Figure 5.9 Diagrammatic representation of the operon and regulator-gene system as a steady-state mechanism.

structural genes under its influence commence to code their characteristic mRNA. Thus, β -galactosidase and two associated enzymes (in our model) are produced, and the β -galactosides are attacked. With the disappearance of the substrate, the system returns to its former operation, that is, the repressor substance turns off the operator, and enzyme production by the structural genes ceases.

Although this model is based on work performed upon microorganisms—and it has not yet been shown that comparable systems are widespread in the cells of the more complex organisms—it constitutes a very promising hypothetical explanation of cellular regulation. At least, it is possible to visualize how genes might be turned on and off, and how some cells produce certain substances which other cells do not produce. Because the type of work involved is very tedious, it will probably be some years before the full significance of the operon concept will be known, but it is a start toward solving some extremely difficult problems in regulation and control.

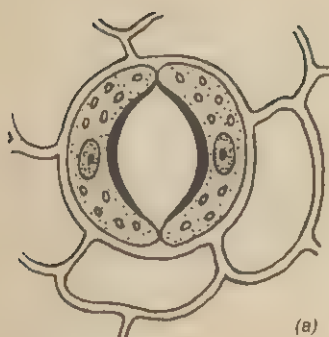
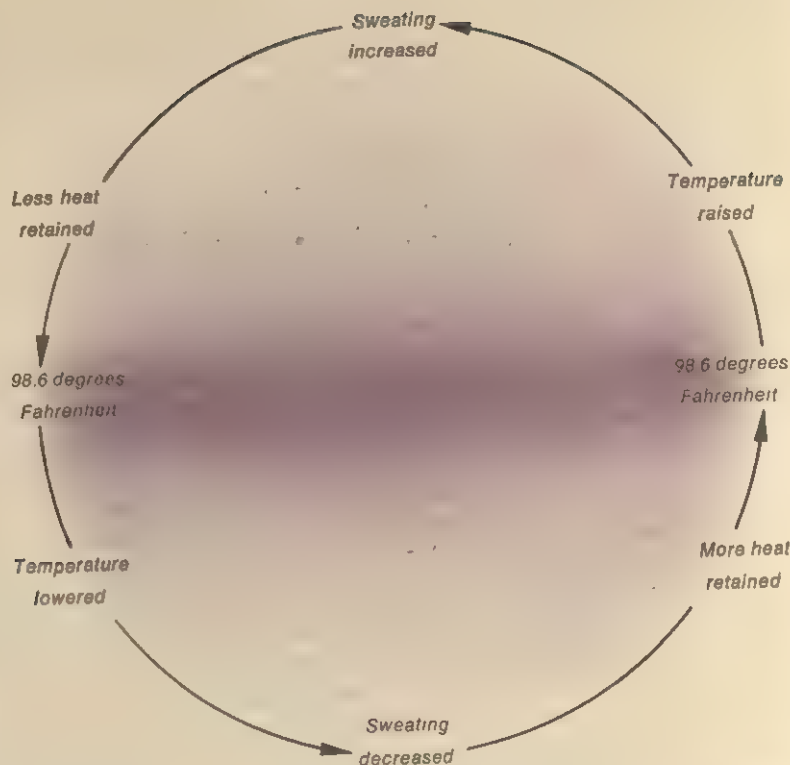
Whether the details of such regulation as we have just described are accurate or not, let us note that the operon system is a homeostatic mechanism. The addition of β -galactosides to the environment

of *E. coli* brings about the production of β -galactosidase, which brings about the degradation of β -galactosides, and so on (Figure 5.9). This is only one of many steady-state controls which apparently exist at the cellular level of organization.

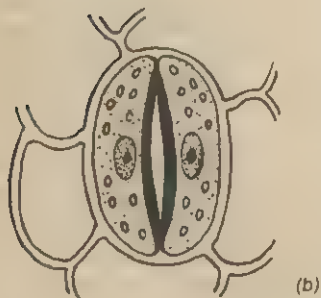
5.3 Regulation and control at the organismic level Since a complex organism is composed of cells, many regulation and control mechanisms found at this organizational level are extensions of such mechanisms as we have presented which are operative in cells. This is particularly true of metabolic activities, which we shall consider in Chapter 6. It is also undoubtedly true of embryonic development, especially in early stages. Furthermore, genes exert their effects in the development and function of organisms through the composite effects of cells, and many effects in the more complex animals are a direct reflection of cellular control. We shall have occasion to refer to some of these effects later on. However, certain other mechanisms are best interpreted as emergent qualities which come about as a result of increased specialization of cells and a coordination of their activities in tissues, organs, and organ systems. In other words, a homeostatic mechanism is not necessarily a mere summation of many homeostatic mechanisms at the cellular level; it may be an expression of the entire organism taken as a whole. Withal, the examples which are presented below fall into this category.

One of the clearest examples of homeostasis in animals is seen in the birds and mammals with regard to the regulation of body temperature. You will recall that only these animals are warm-blooded. The homeostatic mechanism involved is a *temperature-regulating center* located in the hypothalamus of the brain. It is a small mass of nerve cells which connect with effectors at the surface of the body, and it is extremely sensitive to changes in temperature. In man, for example, it responds differently to temperatures above and below about 98.6 degrees Fahrenheit. Let us suppose that a person is situated in a room where the temperature is 100 degrees. As soon as body temperature increases, the temperature-regulating center sends nervous impulses to the sweat glands of the skin, causing them to secrete moisture to the outer surface of the body. Evaporation of the moisture lowers the body temperature, and a drastic rise is thus prevented. When the internal temperature falls below 98.6 degrees the center causes the sweat glands to be less active, and loss of heat from the body is prevented. Here we have a homeostatic system (Figure 5.10). Of course, there are many other factors involved in temperature homeostasis of the human, such as shivering, stimulation of the conscious areas of the brain in regulating clothing, and so on, but even with these added complications, the temperature-

Figure 5.10 Diagrammatic representation of the temperature-regulating center of man as a steady-state mechanism.



(a)



(b)

Figure 5.11 (a) Stoma open because of the turgidity of the two guard cells. Note thickened inner walls of guard cells (b) Stoma almost completely closed because of the loss of turgidity on the part of the guard cells.

regulating center is a homeostatic system. We have oversimplified it only for purposes of illustration.

A good example of homeostasis may be seen in plants, with regard to water-conserving mechanisms. The leaves of most plants exhibit numerous *stomata*, or openings, which are surrounded by *guard cells* (Figure 5.11). These are usually located on the lower surfaces of leaves. Under normal conditions of moisture availability, water travels from the roots to the leaves through xylem tissues, and evaporates from the leaves through the stomata. This process, called *transpiration*, provides a constant supply of minerals and water to the leaf, where these materials become involved in synthetic reactions. (Most of the water passes on out of the leaf, but some is retained.) Certain complex factors in the plant interact in such a way that the stomata ordinarily are open in the daytime, when gaseous exchange from the leaf to the atmosphere is important to photosynthesis, and they are closed at night. The opening and closing of stomata are directly controlled by the guard cells, which are so constructed that they spread apart when they are *turgid* (tightly packed with water) and they come together when they are *flaccid*

(turgor pressure reduced). However, even in the daytime, stomata may close if more water is removed from the leaves than can be replaced from the soil. This might occur by mid-morning under drouth conditions, for example, with the result that the leaves of the plant wilt. Under these conditions, all cells of the leaf, including guard cells, become flaccid, and the stomata are thus closed. This reduces loss of water by transpiration to a great extent, and makes it possible for the plant to regain normal turgidity in its leaf cells. The guard cells and stomata constitute a homeostatic mechanism with regard to moisture; like temperature in birds and mammals, moisture controls its own steady state as long as it has a mechanism for doing so (Figure 5.12).

Such examples as these could be multiplied greatly; both plant and animal physiology are replete with examples of steady-state controls at the organismic level. Perhaps these are sufficient to demonstrate the principle we seek to clarify at this point, and as we proceed through the next several chapters, we shall identify other homeostatic mechanisms of a similar nature.

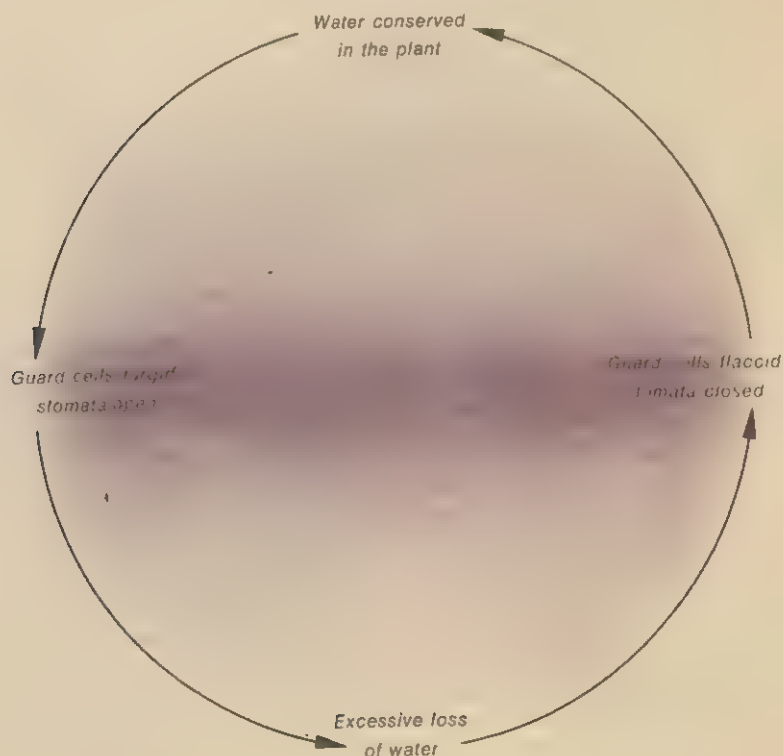


Figure 5.12 Diagrammatic representation of a water-conserving mechanism in plants, as it operates in steady-state control.

5.4 Regulation and control in complex organisms

It might be thought that homeostatic mechanisms are limited to protoplasmic systems contained within single organisms, but such is not the case. Perhaps they are more clear-cut and precisely demonstrable at the levels we have just discussed, but a close study of organisms in nature has revealed that steady-state controls exist *among* organisms as well as *within* organisms. We shall be in a better position to appreciate the significance of homeostasis in nature after we gain some insight into ecology and evolution (Chapters 10 and 11), but it is in order that we illustrate the principle here.

Intraspecific regulation and control Even a casual observer is aware that members of a given species vary greatly in a number of respects. As an example, let us consider one fluctuation which is readily measurable, namely, size. If one traps and weighs a large number of adult field mice, for example, it will be seen that the greatest numbers will cluster around some *mean*, or average, and that numbers taper off toward weight extremes in either direction (Figure 5.13). Of course, such data might be interpreted in a number

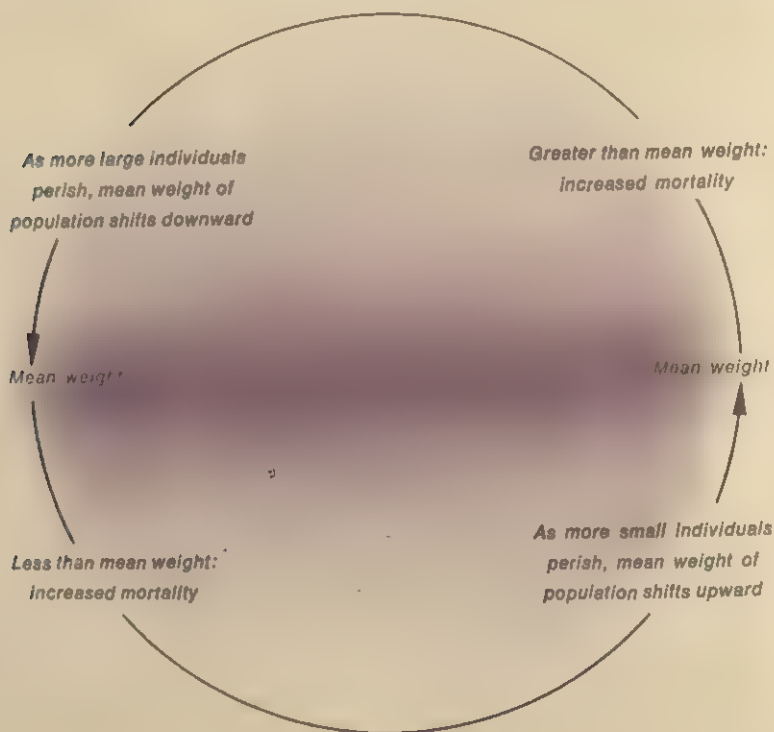


Figure 5.13 Diagrammatic representation of steady-state control in a population of animals

of ways, but on the basis of many precise studies it appears that a given species of animals tends toward some norm which is apparently right for that animal in its environment.* Now this might come as a surprise to most of us, since we tend to equate size with superiority, but such is not necessarily the case. For example, added size might well impart a disadvantage to an animal in remaining hidden from a predator, or if it is a predator, extra weight might slow it down to such a point that it could not compete successfully for its prey.

The tendency of a population† to cluster around a weight mean is best interpreted homeostatically (Figure 5.13). Assuming that its chance for survival is best at the mean weight, and this is apparently the case, mortality increases as one departs from the mean in either direction. Because animals near the mean weight become more involved in reproduction than do those which fluctuate from it, there is a continued tendency (since hereditary factors are involved) for the population to remain clustered around the mean. The entire system is homeostatic, as shown in Figure 5.13, because weight extremes cause a shift toward the mean, or "fittest," weight.

However, this raises an important question. Why are the less fit weights not eliminated altogether? This question can be answered in terms of genetics and evolution, and here again, we lack sufficient insight at this point to appreciate most of the implications. Suffice it to say at this point that genes which influence the development of less fit traits in an organism may persist for a long time in a population, and for all practical purposes, we can always expect some variation.

Interspecific regulation and control Perhaps you have heard the expression "balance of nature." This is a clumsy and oversimplified statement of a homeostatic mechanism which is indeed operative in nature, but which hardly keeps populations in balance. Actually, nature as a whole has never been in balance, and it never will be. Only isolated segments of interacting populations demonstrate anything resembling a balance, and even here, close studies reveal continuous fluctuations.

Nevertheless, interacting species demonstrate some rather interesting homeostatic mechanisms. Like the factors which operate in stabilizing a population at a mean weight, these mechanisms tend to maintain the status quo. Without them, there would be no semblance of a balance at all.

* The same principle is generally valid for plants, but since we are obliged to deal with the complication of continuous growth in plants, we shall restrict our discussion at this point to animals.

† Ecologically a population is a group of individuals belonging to the same species which occupy some definite environmental area.

Let us consider a particularly well-studied case of interspecific homeostasis, that of the Canadian lynx (*Lynx canadensis*) and the snowshoe hare (*Lepus americanus*). Beginning in the year 1736, the Hudson's Bay Company kept records on the number of lynx pelts taken by trappers in Canada, and it soon became apparent that peak numbers occurred every ten years. Subsequent observations revealed that the snowshoe hare population peaks stayed slightly ahead of those of the lynx population. It has been determined that the hare population fluctuates at ten-year intervals with or without the lynx, and apparently this is a result of a complex of factors. However, the relationship of the lynx cycle to that of the hare is readily explained. Since the lynx preys chiefly upon the snowshoe hare, its fortunes rise and fall with the hare population. In this fashion, the lynx population is subject to a form of homeostatic control.

Although few examples of interspecific homeostasis are as well-documented as that presented above, this form of control is widely operative in nature. In many cases, the relationships are extremely complex, especially where more than two species are involved. For example, a food web (Figure 10.11) demonstrates homeostasis among a possible complex of many organisms.

5.5 Summary Homeostatic mechanisms are operative at all organizational levels of living matter, and recognition of the steady-state principle enables us to understand partially how complex systems achieve balance and organization. At the cellular level, nuclear control of the cell is achieved through the DNA-RNA-protein synthesis mechanism, although homeostasis at this level is more difficult to demonstrate than at higher levels of organization, the operon model affords one possible explanation. At the organismic level, a large number of homeostatic mechanisms are known, especially among the more complex organisms. Representative of these are the regulation and control of temperature in birds and mammals and that of water conservation in the more complex plants. Above the organismic level, regulation is maintained within populations by the tendency of individuals to maintain proximity to a mean, or fittest average, for a given trait. In intraspecific relations, a balance may frequently be demonstrated between or among different species, especially in predator-prey relationships. This was illustrated in this chapter by the related fluctuations of the Canadian-lynx and snowshoe-hare populations in Canada.

Questions 1 Early in the chapter, we declared that a living organism is in a steady state. A little later, the statement is made that a (living) system

is steady only when it is dead. Are these two statements in conflict? Explain.

2 At this point in your course, how would you define a gene?

3 An amoeba deprived of its nucleus can live for several days, but unlike normal amoebas, it cannot increase in mass and divide to form two amoebas. How do you account for this loss of synthetic ability?

4 Summarize the work of Hämmerling on *Acetabularia* presented in this chapter and tell something of its significance.

5 Distinguish among mRNA, rRNA, and tRNA. How does each contribute to regulation and control within a cell?

6 Return to the end of Chapter 3 and consider Question 2 again. Can you add anything to the answer you gave at the time you first considered this question?

7 If the body temperature of a human being rises to about 107 degrees Fahrenheit, the temperature-regulating center ceases to function, and the temperature continues to rise until death results even if the cause of the temperature rise is removed. Conversely, the center is incapacitated at about 85 degrees Fahrenheit, and death may occur from freezing. In the case of either extreme, we say that "positive feedback" has taken over. In the normal functioning of the center, what would the term "negative feedback" mean?

8 If the nucleus is removed from one of the cells of a very young frog embryo consisting of only two cells and is replaced by a nucleus from an embryo consisting of a few hundred cells, development proceeds normally. However, if a nucleus from a cell of a much later stage of development is transplanted into such a young cell, development is highly abnormal. Offer a tentative explanation based on the operon concept of gene action.

9 Explain the tendency of a population of animals to cluster around a weight mean in terms of homeostasis.

10 Quite frequently, eradication of snakes in a given area results in a tremendous increase in the number of rats and mice. Apparently, the reverse is not the case, that is, eradication of rats and mice does not cause a reduction in the numbers of snakes. Explain this apparent complexity in balance-of-nature homeostasis.

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In addition to these books, a number of articles from *Scientific American* bear on the subject of control and regulation, especially at the cellular level. Most of those recently published which are appropriate to this chapter are included in *The Living Cell* (see the reference at the end of Chapter 3).

Metabolism

As we have noted, living organisms are characterized by certain structural and functional features which set them apart from the nonliving world. One of these features is the phenomenon of metabolism (Gr. *metabol*, change + *ism*, the process of). In the broadest sense, metabolism refers to the sum total of all the chemical changes or reactions which take place in a living organism. However, the term is often used in a more restricted sense to include only those chemical reactions which occur within individual cells. According to this definition, then, metabolism is entirely a cellular phenomenon, and the term can be applied to a multicellular organism only in the sense that it exhibits multiple cellular characteristics. This viewpoint would not take into consideration any aspects of organismic metabolism which might consist of emergent properties.

For our purposes, we shall regard metabolism in its broadest sense, that is, as a characteristic of the organism with regard to its total chemical activity. Of course, this includes cellular activity, but it also takes into consideration a number of phenomena which are not simply a sum of metabolism at the cellular level. After all, it is the whole organism which achieves homeostasis in its environment, and this must be taken into account.

Essentially, metabolism (whether at the cellular or at the organismic level) consists of three phases: *nutrition*, *synthesis*, and *respiration*. Nutrition is that aspect of metabolism by means of which the raw materials for synthesis and respiration are supplied. Synthesis (sometimes called *anabolism*) is that aspect of metabolism during which protoplasm or protoplasmic components are constructed from the raw materials supplied in nutrition. Generally speaking, the chemical reactions which are characteristic of this phase of metabolism are "energy-consuming," that is, they exhibit a $+\Delta F$. Respiration (sometimes called *catabolism*) is that aspect of metabolism in which the raw materials supplied in nutrition are degraded, or broken down, and chemical energy residual in such materials is made available to the cell or organism. In general, the chemical reactions which are characteristic of this phase of metabolism are "energy-yielding," that is, they exhibit a $-\Delta F$.

Before entering into the body of our discussion, let us make one additional point. It might seem that we are indulging in circular reasoning by stating that metabolism is a characteristic of living organisms which sets them apart from the nonliving world, and then proceeding to define metabolism as the sum total of the chemical activity which occurs within a *living organism*. Obviously, chemical activity can take place outside a living organism (*in vitro*). It would appear that we are in the rather awkward position of partially defining life in terms of metabolism, and in turn, defining metabolism on the basis of its occurrence within a living system.

This apparent paradox may be solved by considering the material

of Chapter 5. A living organism is capable of continued metabolism because its metabolism is precisely controlled. The processes of nutrition, synthesis, and respiration not only must take place within a living organism but they must occur in a certain relationship to one another. In other words, these three phases are regulated by one another, and in this sense, they are in balance. Herein lies the difference in the chemical activity we call metabolism, and chemical activity which occurs in test tubes. Metabolism is precisely controlled and ordered, and is thus inherently self-perpetuating. This, within itself, is an excellent example of steady-state control which we discussed in Chapter 5. Continued metabolism is a result of control, and at the same time, the control mechanisms are dependent upon continued metabolism. For example, DNA directs the synthesis of enzymes, and these same enzymes catalyze the chemical reactions which provide the energy and specific raw materials for the synthesis of DNA.

Perhaps an analogy will serve to clarify the matter. Let us consider a mechanical apparatus, say, a gasoline engine. The operation of the engine is analogous to metabolism, the fuel supply is analogous to nutrition, the combustion of this fuel is analogous to respiration, and maintenance or repair of the engine is analogous to synthesis. Obviously, each of these processes must be precisely geared to the others if the engine is to run for very long. In other words, controls must be built into the engine whereby each aspect of its operation "considers" the other aspects. For example, it is not enough merely to lead a gasoline line to the engine, the fuel must be injected into a combustion chamber in precisely the right amounts and at the right times for the engine to run smoothly.

Like all analogies, this one is valid only to a point, but in this case, we are very interested in the point at which it breaks down. An engine is not inherently capable of repair (synthesis). It cannot take a broken piston and use fuel to make a new one because it lacks the organization and control for doing so, and this is the essential difference between nonliving and living systems. In the living system, metabolism runs the machinery of the organism, and continued metabolism is made possible by the running machinery. In the final analysis, it is really this property that we call life, and we might even define life as *controlled metabolism*.

In summary, metabolism is a very inclusive term. Controlled metabolism is at the same time the cause of, a part of, and the result of those characteristics of life to which we shall devote subsequent chapters. Perhaps you now see, if you did not do so previously, why we said in our introduction to Chapter 5 that living systems might be characterized by a single word, *complexity*.

Metabolism
at the cellular
level

6.1 We have chosen to present the material of this chapter within the framework of separate considerations for cellular and organismic metabolism. Actually, the interdependence of these two levels is such that this is a rather artificial distinction. However, it seems logical to consider nutrition, synthesis, and respiration at the cellular level before elaborating on these phases at the organismic level.

Nutrition Broadly speaking, any substance that may be brought into the cell and utilized in chemical reactions is a nutrient material. Three classes of nutrient materials are required by cells, and by organisms: (1) organic compounds, (2) inorganic materials, chiefly salts, and (3) water. However, cells vary greatly in their relative requirements for these nutrients, especially with regard to organic compounds.

For the moment, let us ignore any nutritional distinctions between complex organisms and consider the requirements of cells themselves. Nutritionally speaking there are basically two types of cell: those which are dependent upon their environment for organic fuel molecules and those which manufacture their own. The latter type of cell is found only in autotrophic organisms, whereas the former type is found in all complex forms, autotrophic or otherwise. Not all cells of a multicellular green plant, for example, carry on photosynthesis; those which do not do so depend upon photosynthetic cells within the same plant for their organic nutrients. In heterotrophic plants and in animals (phagotrophs), of course, each cell must receive oxidizable organic compounds from a source external to the organism of which it forms a part.

Since we shall discuss the utilization of inorganic materials and water in a later topic, let us concentrate momentarily upon the organic nutrients and their role within the cell. Whether such compounds are formed within the cell which utilizes them as an energy source or whether they are transported in, they serve two major functions: They may be chemically "shattered," in which case free energy is made available to the cell, or the carbon chains may be used as building blocks in synthetic processes. The major organic nutrients are carbohydrates, lipids, and proteins. Under certain circumstances, each of these types may be utilized as energy sources, or again, each may be utilized in synthetic reactions. Generally speaking, however, the carbohydrates and lipids are "preferred" by the cell as energy-yielding compounds, and protein functions chiefly in synthesis.

In actual practice, there is a rapid turnover in the cell of all organic molecules except for certain ones such as those of DNA which

are somewhat isolated from the enzymatic machinery. This means that virtually everything in the cell is a fuel substance in the final analysis. To draw an analogy, let us suppose that a certain lumber dealer finds it necessary, for some reason, to keep a fire going in a furnace. Under ordinary circumstances, he uses coal or oil as fuels because they are cheap and readily available. He might use the furnace, since he has it anyway, to dispose of scrap lumber and assorted waste products, but he does not depend upon these for fuel. They are only *incidentally* burned. Now let us assume that his supply of coal and oil is cut off. He might be forced to use whatever he can find that will burn, and if maintenance of his fire is sufficiently important to him, he might even be obliged to burn his own valuable lumber. Of course, this analogy is only a rough one, since we do not ascribe consciousness and purpose to the cell as we do to a human being, but there are valid parallels. The coal and oil are analogous to carbohydrates and fats, the lumber to proteins, and the scraps of material to the various "used" molecules of the cell which are disposed of in the metabolic "fire."

Even though we cannot draw an exact distinction between fuel and nonfuel compounds, the original distinction is valid for all practical purposes. Carbohydrates and fats are the only materials that furnish energy to the cell in very large amounts, at least under most conditions. Proteins may or may not play a significant role in this respect, depending upon their quantity and the relative quantities of the other two fuels. Any other organic molecules that are broken down may yield some energy, but in amounts that are quite insignificant when compared with that furnished by carbohydrates, fats, and proteins.

At this point, let us consider how nutrient materials get into cells. Of necessity, these materials are present in the environment of the cell. Depending upon the particular type of cell, this environment may consist of pond water, the general atmosphere, or some form of body fluid such as blood. It may also include other cells. Regardless of the general environment, a cell is almost always surrounded by some aqueous medium, even if this medium exists only as a thin film separating closely-packed cells. The aqueous medium is in direct contact with the cell membrane, even if the cell possesses a wall (you will recall that plant cells are generally enclosed within a cellulose wall, this wall is permeable to all substances in aqueous solution). Most of the problems associated with understanding *absorption* (the movement of nutrient materials into cells) involve a consideration of the structure and function of cell membranes. In addition, the nature and concentration of the nutrient substances which are absorbed must be considered.

The cell membrane has sometimes been pictured as a passive barrier containing pores which admit small particles and reject large ones. That the membrane is porous to a degree seems evident, and in general, small molecules are absorbed more readily than large ones. However, this view of the membrane is highly misleading, because several factors govern the passage of substances across it. Apparently, the major factors involved in absorption are *osmosis*, *diffusion*, *electrical charge*, *solubility in lipids*, and *active transport*.

Osmosis may be defined as the movement of water from a region of relatively low concentration of dissolved substances into a region of relatively high concentration across a membrane which is impervious to at least some solute particles. A balance of water between the cell and its environment seems to be at least partially explicable on the basis of osmosis. For example, if the concentration of dissolved substances is greater within the cell than in its surroundings, some water is absorbed into the cell through osmosis. In such a situation, the solution outside the cell is said to be *hypotonic* to the solution within the cell, and conversely, the solution inside is said to be *hypertonic* to that outside. If the two solutions are equal to each other in concentration of dissolved particles, they are said to be *isotonic*, in which case there is no net movement of water across the membrane.

In order to demonstrate that living cells are subject to pressure changes associated with osmosis, let us consider a cell such as that of *Spirogyra* (Figures 4 25, 6 1), a filamentous green alga which thrives in ponds of fresh water. Although its surrounding medium is never absolutely pure water, it is nevertheless hypotonic to the protoplasmic contents of the cell. There is thus a continual tendency for osmosis to occur inward. Why, it might be asked, does the cell not increase in size until it bursts? The reason lies in the rigidity of the cellulose cell wall, which is sufficient to resist bursting under these conditions. Enough pressure builds up inside the cell to establish an osmotic equilibrium. Whenever a cell exhibits an internal pressure due to osmosis, it is said to be *turgid*, and such pressure (resulting from osmosis) is called *turgor pressure*.

Now suppose that a filament of *Spirogyra* (Figure 6 2a) is put into a solution prepared by dissolving five grams of sodium chloride in sufficient water to make the entire solution equal one hundred milliliters (about one-fourth pint). This solution proves to be hypertonic to the protoplasm of the cells, and within a matter of seconds sufficient water leaves a given cell to cause a shrinking of the protoplast. The cell wall, being rigid, remains in place and the plasma membrane actually draws away from it (Figure 6 2b). This loss of turgidity on the part of the cell due to osmosis is called *plasmolysis*.

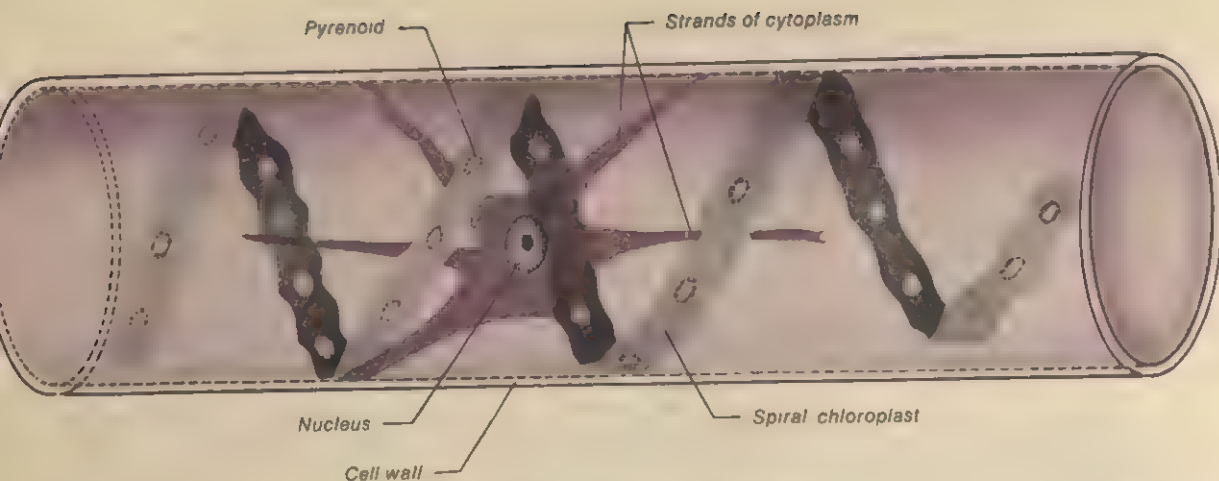


Figure 6.1 Diagrammatic representation of a cell of *Spirogyra*. Note the spiral chloroplast, which is imbedded within the peripheral cytoplasm surrounding a large central vacuole. Some species have more than one chloroplast per cell. Compare with Figure 4.25.

and a cell whose turgidity is less than that experienced in its normal environment is said to be *flaccid*. Unless plasmolysis has occurred to a critical degree, normal turgidity may be restored to the cells of the *Spirogyra* filament by replacing the sodium chloride solution with pond or tap water, thus reversing the direction of osmosis (Figure 6.2c).

Many freshwater organisms which do not possess rigid cell walls manage to withstand turgor pressures by "bailing out" excess water. *Amoeba* and *Paramecium*, for example, have *contractile vacuoles*, which function as pumps in this respect (Figure 4.2). Were it not for this mechanism, such delicate cells would soon burst. In higher animals, cells are surrounded by fluids which are isotonic to the protoplasm. The delicate red blood cells of man, for example, can be made to swell and burst if removed from their normal environment and placed in a solution which is even slightly hypotonic to them.

Although water itself is not an energy-yielding substance, it is of paramount importance to the metabolic life of cells, and hence to organisms, in that it serves as a solvent for and a carrier of a variety of compounds both inside and outside the cell. Not only is this the case, but it makes possible enzymatic reactions which could not occur otherwise. Furthermore, its molecules actually enter into certain metabolic reactions.

Diffusion is the net movement of particles (molecules, atoms, or ions) resulting from their tendency to be distributed evenly through-

out a given space. In a sense, it is an exemplification of the second law of thermodynamics in that particles tend toward a random distribution within their particular system.

For example, if a vial of perfume is opened at the front of a room, its odor may be detected at the back of the room within a short time because of the passage of its molecules through the air. At least some substances dissolved in water seem to be absorbed into cells by diffusion, thus, if the concentration of dissolved materials is greater in the surrounding medium than within the cell some of these materials may be absorbed. The exchange of such gases as oxygen and carbon dioxide between the cell and its environment is apparently due primarily to diffusion.

Let us note that since the movement of water into a cell (osmosis) is a function of the concentration of dissolved particles on both sides of the cell membrane, any force which affects the concentration of dissolved particles will also affect osmosis. As a consequence, diffusion and osmosis are closely related phenomena, with diffusion having a direct effect upon osmosis. This (among other considerations) indicates that osmosis is a much more complex phenomenon than the mere differential movement of water molecules based upon their relative concentrations alone.

It has been observed that charged particles enter the cell less

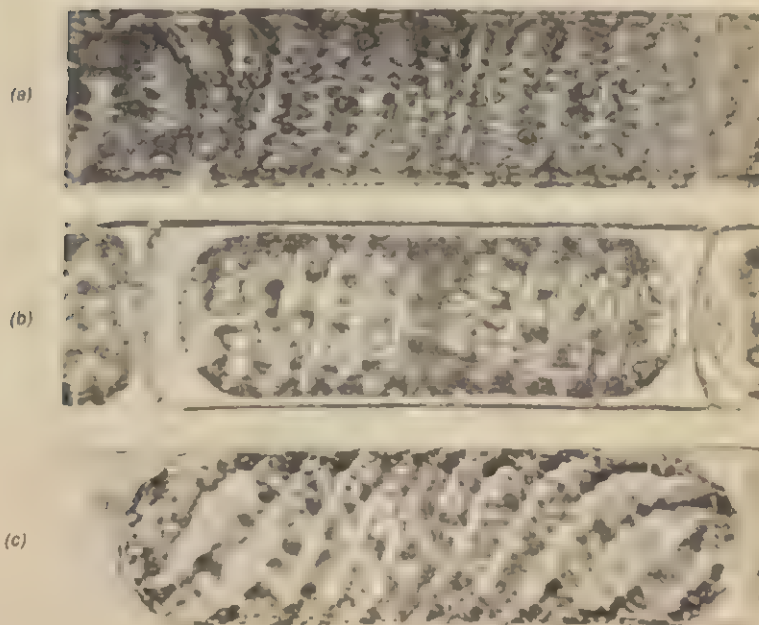


Figure 6.3 Plasmolysis in *Spirogyra*.

(a) Appearance of a cell growing in pond water. (b) Appearance of the same cell about 30 seconds after it was surrounded by 5 percent sodium chloride. Note that the protoplast, bounded by the plasma membrane, has pulled away from the cell wall. (c) Deplasmolysis of a cell, accomplished by surrounding a plasmolyzed cell with tap water. Note that the protoplast is returning to its normal position.

readily than uncharged ones. As a rule, the greater the charge the less freely a particle moves across the cell membrane. For instance, such monovalent ions as K^+ and Cl^- enter the cell more readily than divalent or multivalent ones, for example, Mg^{++} or SO_4^{--} . This phenomenon is probably best explained by the nature of the proteins present in the cell membrane. In general, protein molecules are highly charged, and thus tend to repel charged particles.

Still another factor known to be involved in absorption is the degree to which a substance is soluble in lipids. For example, the higher (more complex) alcohols are more lipid-soluble than the lower alcohols, and in spite of their greater size and complexity, the higher alcohols penetrate the cell membrane more readily than the lower ones. It has been postulated that since lipid materials constitute a large proportion of the cell membrane, such substances as the higher alcohols are more readily accepted by the membrane than less lipid-soluble materials.

Of all the factors which influence the passage of nutrients through cell membranes, active transport is probably the most important, and at the same time, the least understood. As the name implies, active transport involves the passage of a substance through the cell membrane with an expenditure of energy on the part of the cell. In other words, a metabolic process is involved, and the cell is obliged to perform work in transporting many substances to its interior. There are numerous examples of ions and large molecules exhibiting low solubility in lipids being transported into the cell against an electrical and a concentration gradient. Furthermore, if in such cases a metabolic poison is administered to the cell, transport ceases, which indicates that transport of these materials is dependent upon the processes of metabolism. For example, a cell usually maintains a high concentration of potassium (K^+) ions within the cell membrane, and a high concentration of sodium (Na^+) ions outside the membrane. Work is required on the part of the cell in keeping such ions from establishing an equilibrium on both sides of the membrane. Although relatively little is known about the precise mechanisms involved in active transport, it appears that it is a very complex phenomenon, and one that is highly important in a wide variety of absorption phenomena.

In addition to the five factors which we have discussed, cells occasionally take in relatively large droplets of materials by a process called *pinocytosis* (Gr. *pino*, to drink + *cyton*, cell). For example, many cells "drink" or "gulp" fluid materials from their environment, as a result of which certain large molecules in solution may be taken into the cell. Furthermore, cells of multicellular animals have been observed to ingest relatively large particles of organic

matter in similar fashion to the feeding habits of an amoeba. This phenomenon is called *phagocytosis* (Gr. *phagos*, to eat + *cyton*). For example, certain white blood cells of the complex animal body engulf bacteria or various particles and digest them. Pinocytosis and phagocytosis may be considered to be special cases of active transport.

In summary, absorption is a complex phenomenon, and it frequently involves chemical changes and energy transformations at the surfaces of cell membranes. It is highly important, therefore, that we conceive of the cell as an extremely active unit which maintains lines of exchange with its surrounding medium. Without these lines of exchange, it would be impossible for the cell to carry on the vital functions of synthesis and respiration, which are discussed below.

Synthesis As we have indicated, synthesis is that aspect of metabolism in which the components of protoplasm are built or synthesized from nutrient materials coming into the cell. This involves the manufacture of structural and enzymatic proteins, nucleic acids, lipids, carbohydrates, and various other types of molecules. In all types of cells, synthesis involves the construction of the basic macromolecules of living systems from simpler nutrient substances, and the chemical reactions involved are primarily endergonic, that is, they exhibit a $+\Delta F$.

It is convenient to classify synthetic reactions according to the source of the energy involved. *Photosynthesis* includes those reactions occurring in cells containing chlorophyll in which an external energy source, sunlight, provides the energy. Such reactions combine the raw materials carbon dioxide and water in the formation of carbohydrates. *Chemosynthesis* involves the oxidation of certain inorganic compounds such as H_2S and NH_3 as an energy source, and this energy is utilized in the synthesis of complex compounds from simple raw materials. Finally, *organosynthesis* includes those reactions which depend upon an internal energy source, namely, that derived from respiration (see topic below). Of these three classes of synthetic reactions, organosynthesis is by far the most common in that it is characteristic of all cells. In contrast, photosynthesis is limited to cells which contain chlorophyll, and chemosynthesis is limited to the cells of certain microorganisms. It should be pointed out that while the synthetic reactions themselves are energy-consuming ($+\Delta F$), and the reactions upon which we are basing our classification are energy-yielding ($-\Delta F$), it is more meaningful to classify synthetic reactions from the standpoint of the decompositional reactions which provide the energy for synthesis. This is a reflection of the intimate relation between synthesis and respiration; actually, it is difficult to discuss these two aspects of

metabolism separately. Hence, much of what we say about synthesis will be applied later on to respiration.

Before we discuss the types of synthetic reactions we have introduced, let us digress from this topic and discuss some basic molecules and types of reactions involved in energy transformations which occur within cells. At this point, you may wish to read portions of Section 2.3 again, since that material is basic to an understanding of energy transformations as they relate to electron activity in atoms and molecules, to chemical bonds, and to the types of reactions which are involved in energy yield and uptake.

Energy changes in cells result from electron transfers which occur among certain molecules of the cell. Any process whereby electrons are removed from atoms or molecules is called an *oxidation*, and any process whereby electrons are added to atoms or molecules is called a *reduction*. Of necessity, an oxidation is always accompanied by a reduction, that is, the atom or molecule which serves as an electron donor is oxidized, while that which serves as an electron receptor is reduced. In living systems, the removal or addition of electrons may be considered synonymous with the removal or addition of hydrogen atoms, since hydrogen is always (with rare exceptions) involved in cellular oxidation-reduction. Hence, an oxidation-reduction reaction might also be called a dehydrogenation-hydrogenation reaction. An entire oxidation-reduction reaction consists of two *half-reactions*, that is, the oxidation of one molecule and the reduction of another. For example, among the compounds involved in cellular oxidation-reduction are several related compounds called *cytochromes*, designated *a*, *b*, *c*, and so on, for purposes of distinction. Each cytochrome molecule, regardless of type contains a single atom of iron in its structure, and this iron may exist in the ferrous (Fe^{++}) condition or in the ferric (Fe^{+++}) condition. When it exists in the Fe^{++} condition, the cytochrome molecule is in a reduced state; conversely, when it exists in the Fe^{+++} condition, it is in an oxidized state. Thus, as an electron passes from a Fe^{++} cytochrome *b* to a Fe^{+++} cytochrome *c*, cytochrome *b* is oxidized to the Fe^{+++} condition and cytochrome *c* is reduced to the Fe^{++} condition. The two half-reactions and the net reaction are illustrated below:



Oxidation of cytochrome b (half-reaction)



Reduction of cytochrome c (half-reaction)



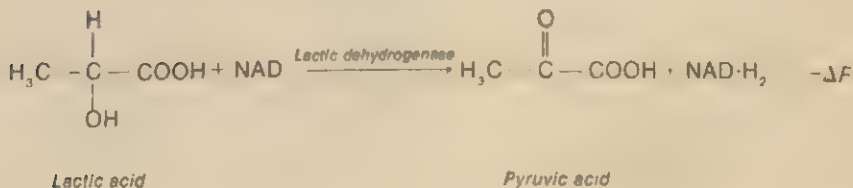
Net reaction ($-\Delta F$ net)

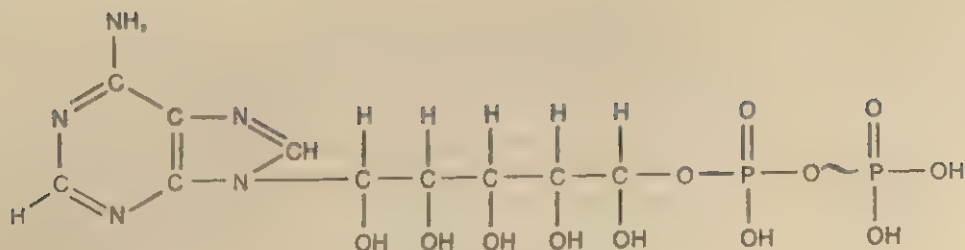
Let us note that it is actually the reductional half of the reaction which is energy-yielding. In fact, the energy is sufficiently great that the entire (net) reaction is energy-yielding. Hence, the products of this oxidation-reduction reaction are more stable than the reactants, and as an electron passes from cytochrome *b* to cytochrome *c*, energy is released.

The cytochromes are usually intermediate compounds in a system of electron and hydrogen transfer reactions, that is, they are neither the initial acceptors nor the ultimate acceptors. Two other kinds of molecules may serve as initial acceptors, they are both members of a class of organic molecules called *coenzymes*, and they function in connection with enzymes which catalyze oxidation-reduction reactions. Specifically, these two types of coenzymes are the *nicotinamides* and the *flavins*. The nicotinamides usually serve as the initial hydrogen acceptors, and they are more common in cells than flavins. The two major nicotinamides are *nicotinamide adenine dinucleotide* (NAD) and *nicotinamide adenine dinucleotide phosphate* (NADP). The major flavin is *flavin adenine dinucleotide* (FAD), in some instances, it serves as an initial hydrogen acceptor, but usually, it is an intermediate acceptor between the nicotinamides and the cytochromes. Later on, when we discuss respiration, we shall illustrate the relationships which exist among these hydrogen acceptors, but for the present, it will be sufficient that we know of their existence.

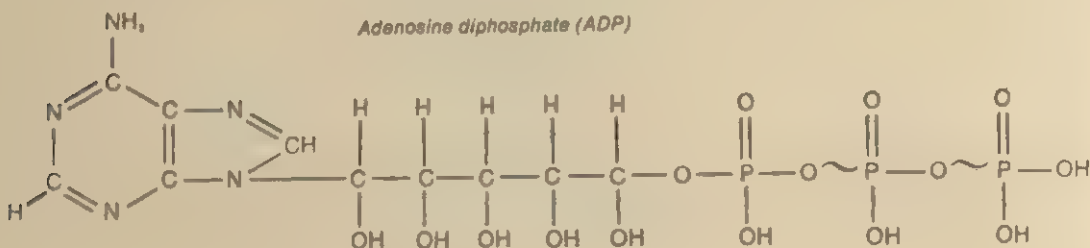
The source of the hydrogen atoms which furnish electrons to oxidation-reduction sequences in cells is somewhat variable. In photosynthetic reactions, electrons are contributed by chlorophyll or water. In chemosynthetic reactions, they are contributed by certain inorganic compounds. In organosynthetic reactions, hydrogen atoms are furnished by organic molecules. As a further example of electron transfer in living systems, let us consider the loss of hydrogen from an organic compound and its transfer to an electron-transporting system.

Lactic acid is an important intermediate compound in certain metabolic systems. In its metabolism, it undergoes dehydrogenation to yield pyruvic acid in the presence of the enzyme lactic dehydrogenase and the coenzyme NAD, as follows:





Adenosine diphosphate (ADP)



Adenosine triphosphate (ATP)

Figure 6.3 Structural formulas of adenosine diphosphate and adenosine triphosphate. The bonds (), of which ADP possesses one and ATP two, signify high-energy bonds. In the ordinary functioning of the ADP-ATP energy cycle, only the terminal high-energy bond of ATP is broken with a release of energy.

Note that in this reaction lactic acid is oxidized (dehydrogenated) to pyruvic acid while the initial hydrogen (electron) acceptor NAD has been reduced to NAD-H. The net reaction is energy-yielding and the end products are more stable than the reactants. (As an exercise, perhaps you can break this reaction down into half-reactions as we did for the oxidation-reduction of cytochrome.)

At this point, let us consider a very important aspect of electron transfer. If we follow the pathway taken by the electrons furnished by lactic acid in the example given above, we find that they are transferred to oxygen, but all along the line, they yield energy to the cell through successive oxidation-reduction reactions. It is necessary that such energy be made available to the cell in small steps; otherwise, it would all take the form of heat. Living cells are not heat engines, and if energy were liberated suddenly in great amounts, a cell would literally burn up. In other words, a cell runs on chemical energy, not thermal energy.

When we speak of a reaction as "yielding" energy, we do so for want of a better term. Actually, only a small part of the energy made

available to a cell is yielded as heat, the remainder is transferred from one type of chemical bond to another. This transfer involves a compound called *adenosine diphosphate* (ADP) which is phosphorylated in the process to form *adenosine triphosphate* (ATP). These two compounds are shown according to their structure in Figure 6.3. The terminal phosphate bond of ATP, which is formed by energy transfer, is called a high-energy bond, and we denote it by a special symbol (\sim). In a sense, it is ordinary (low-energy) bonding in a highly concentrated form. Whenever such a high-energy bond is formed, it is a result of exergonic reactions ($-\Delta F$) which occur in the cell. When it is broken and the energy is transferred to other bonds, the reactions are endergonic ($+\Delta F$). During the process, ATP is dephosphorylated back to ADP. This cycle is shown in Figure 6.4. To return to our original point, energy is not actually "yielded," "released," "utilized," or "expended" in the cell; it is *transferred* and *transformed*.

Now let us relate the ADP-ATP system to our previous discussion of dehydrogenation (oxidation) and its accompanying electron transfers by considering the oxidation of a "fuel" compound. We have shown schematically in Figure 6.5 how high-energy bonds are formed through electron transfer. Let us trace this sequence of events closely.

First of all, the fuel molecule is phosphorylated through reaction with a phosphate source, that is, a radical containing a single atom of phosphorus is substituted on the molecule for a hydrogen atom or a hydroxyl group. It then undergoes dehydrogenation and loses two hydrogen atoms. It will lose its others later on, but we will consider only these two at this point. The hydrogen atoms reduce NAD to $\text{NAD}\cdot\text{H}_2$, and the fuel molecule is thus oxidized. This oxidation of the molecule causes some electrons to shift, and in the process, the phosphate bond becomes a high-energy bond. Almost simultaneously, this high-energy bond is transferred to ADP, thus forming ATP, and the oxidized fuel molecule is in a dephosphorylated state. Meanwhile, $\text{NAD}\cdot\text{H}_2$ passes the hydrogens along to the next acceptor (FAD) in the hydrogen-transport sequence. At this point, the electrons of the hydrogen atoms assume a lower energy level, and the

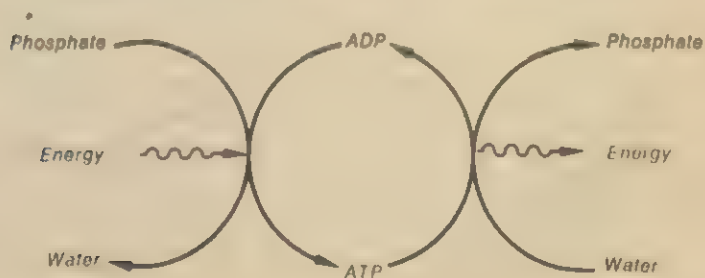


Figure 6.4 The ADP-ATP cycle, by means of which energy transformations are accomplished within cells. Ordinarily, energy coming into the cycle is the potential chemical energy of chemical bonds, and that shown leaving the cycle is kinetic energy as it is expended as heat, movement, the energy utilized in synthesis, and so on.

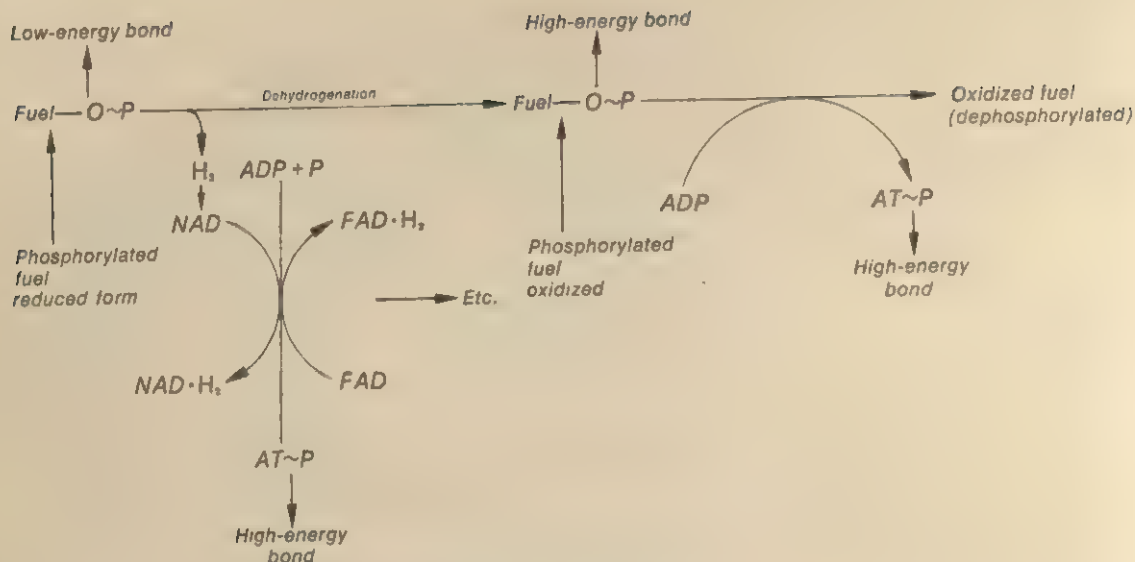


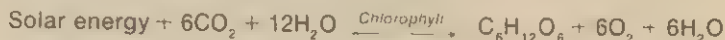
Figure 6.5 The formation of high-energy bonds through electron transfer. See text for amplification.

resulting energy is transferred to a high-energy bond of ATP through the phosphorylation of ADP. At certain points in the sequence, more ATP is generated in this fashion. Some energy dissipates as heat in the process, but much of the energy is transferred to ATP. In a sense, ATP is the "usable currency" of the cell, and it may be used to phosphorylate more fuel or to drive the many endergonic reactions which take place in the cell.

Apparently, the ADP-ATP energy-transfer system is operative in all cells, and its importance to the world of life can hardly be overestimated. In spite of the variety of forms that energy expenditure takes in organisms, ATP is usually involved in all such reactions. The system is quite efficient, inasmuch as energy may be transferred from a fuel substance to ATP in a series of steps whereby heat production (representing energy loss) is held to a minimum. It is worthy of note that living organisms have this mechanism in common, which is an indication that all of them are more nearly alike than superficial differences have often led us to believe.

PHOTOSYNTHESIS With the exception of the small group of chemosynthetic bacteria mentioned earlier, all organisms depend ultimately upon green plants as a source of organic nutrients. For this reason, it is imperative that we consider photosynthesis in our discussion of metabolism. This process occurs whenever radiant energy (usually

sunlight, although artificial light of suitable wave lengths may be employed) is received by chlorophyll molecules. By a series of energy transformations, carbon dioxide and water are combined in the production of carbohydrates and oxygen. A net reaction can be written as follows, using glucose as the carbohydrate:



As we shall see, this is an oversimplified equation. It summarizes a number of separate reactions, and we write it at this point only as a means of visualizing the whole process before examining its separate parts.

For many years after the raw materials and end products of photosynthesis were known, it was thought that carbon and oxygen separated during the process. In such a reaction, carbon would attach to water, and oxygen would be released. The plausibility of this hypothesis can readily be seen if we reduce the equation to its simplest terms:



It was supposed further that the (CH₂O) unit was "multiplied" in some fashion to form sugars. Six such units, for example, might form glucose. As is so often the case in scientific matters, however, the most attractive, plausible, or popular hypothesis does not always turn out to be a fruitful one. During the 1930's, it was demonstrated that some bacteria carried on photosynthesis without the liberation of oxygen (a few species are characterized by photosynthetic pigments), and in the early 1940's, studies using radioisotopic tracers indicated that in green plants liberated oxygen did not come from CO₂. This was accomplished by incorporating "heavy" oxygen (¹⁸O) into water molecules and tracing it throughout the process. Contrary to the earlier idea, it was found that the oxygen of H₂O, not that of CO₂, became the O₂ liberated during photosynthesis. About the same time (1939), the biochemist Robert Hill found that exposure to light of green cells in a test tube in the presence of *hydrogen acceptors* resulted in the liberation of oxygen; but no carbohydrate was synthesized. A little later, it was shown that carbohydrate synthesis would occur in the dark within green cells if they had previously been exposed to light. Thus, it became obvious that photosynthesis involved two phases: the *light*, or *photo*, phase and the *dark*, or *synthetic*, phase. We shall discuss these in order.

The chlorophyll molecule is so constructed that it can absorb "packets" of light energy (photons or quanta) from certain wave lengths of light. In the process of doing so, certain of its electrons become energized and actually leave the molecule. The energized

state of the electrons represents the transferred radiant energy. This process of electron separation leaves the chlorophyll molecule in an ionic state. Eventually, electrons will return to the molecule, but only after their energy of excitation has been transferred elsewhere. Apparently, there are two possible pathways, or cycles, by means of which the electrons may get back to the chlorophyll molecules. Both of these cycles involve oxidation-reduction reactions, and as the electrons are transferred from one acceptor to another, they pass to lower energy levels. In the process, the "excess" energy of the electrons is transferred into high-energy phosphate bonds when ADP is phosphorylated to ATP. Thus, the electrons return to the chlorophyll molecule in a low-energy state, and the oxidized chlorophyll is in a condition to be reduced again. The ATP thus formed may be used as the phosphorylating agent in the synthetic (dark) reactions of photosynthesis.

The cyclic pathways of electron transport outlined above constitute only a part of the light phase of photosynthesis, and it should be noted that the electrons removed initially from chlorophyll are eventually replaced. It should also be noted that in these cyclic pathways the water represented in our initial equation is not involved. Rather,

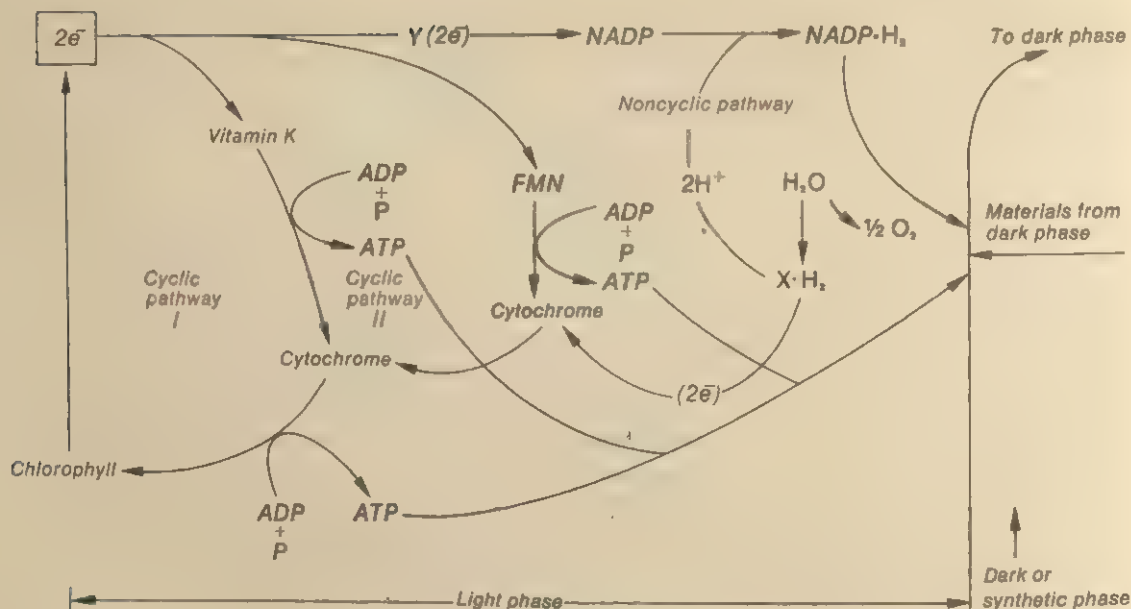


Figure 6.6 Schematic drawing showing the events occurring during the light phase of photosynthesis. See text for amplification. FMN is flavin mononucleotide.

flavins and cytochromes as well as a substance known as *vitamin K* transport the electrons. The role of these acceptors is shown diagrammatically in Figure 6.6. These cyclic pathways leading to the production of ATP are considered to be minor when compared to the entire process of photosynthesis. Furthermore, green plant cells also carry on respiration, discussed in a later topic, in which a relatively high yield of ATP is achieved. Thus, ATP production in the cells is by no means limited to the light phase of photosynthesis.

At this point, let us return to a consideration of the overall photosynthetic equation. It should be apparent now that the products of the reaction, oxygen and carbohydrates, are formed by the splitting of water molecules. Thus, the hydrogen so released reduces the carbon dioxide to carbohydrate, and molecular oxygen is produced. Here again, we are involved in an oxidation-reduction reaction, but one which is highly unlikely from a thermodynamic viewpoint. The problem is this: a weak oxidant (CO_2) must oxidize a weak reductant (H_2O) producing a strong oxidant (O_2) and a strong reductant (carbohydrate). In other words, the CO_2 and H_2O are much more stable than the O_2 and the carbohydrate. In fact, it has been determined that about 112,000 calories* of energy are required to reduce a gram-molecular weight of CO_2 . These reactions constitute the noncyclic pathway of the light phase of photosynthesis. As the hydrogen atoms reduce CO_2 in another oxidation-reduction reaction, the synthetic (dark) phase of photosynthesis begins. At this point, the hydrogen atoms are raised to such an energy level by the energy in the terminal bond of an ATP molecule that they are able to reduce the CO_2 . The ATP molecule involved in any given reaction may have resulted from the cyclic pathways of the light phase, or it may have been generated by some other process.

This latter pathway is said to be noncyclic because the electrons do not cycle back into the chlorophyll molecule as in the two cyclic pathways described above. The noncyclic pathway is shown relative to the two cyclic pathways in Figure 6.6, which depicts the entire light phase of photosynthesis schematically. In summary, light energy and water are fed into the light phase, and the products are ATP, $\text{NADP}\cdot\text{H}_2$ and O_2 .

Essentially, the dark phase of photosynthesis involves the fixation, or reduction, of carbon dioxide in the formation of carbohydrates. Within recent years, this process has been worked out in rather intricate detail, primarily by the use of radioactive isotopes.

* A calorie is a unit of energy, and is equal to the amount of heat necessary to raise the temperature of a gram of water 1 degree Centigrade. The large Calorie, always capitalized in print, represents a thousand small calories. Human physiologists and nutritionists generally use the large Calorie as a unit of heat measurement.

The technique itself involves labeling carbon dioxide with $^{14}_6\text{C}$, feeding the labeled CO_2 to the green cell, and isolating various chemical fractions at different intervals. By this means, the synthetic phase of photosynthesis has been greatly clarified, and the scheme outlined below is now generally accepted.

Carbon dioxide joins a five-carbon sugar, *ribulose diphosphate* (RDP), which is already present in the cell, to form a very unstable six-carbon compound. This six-carbon compound has a very brief existence; almost immediately it breaks down spontaneously into two molecules of a three-carbon compound, *3-phosphoglyceric acid* (PGA). Each molecule of PGA is then reduced to the aldehyde form, *phosphoglyceraldehyde* (PGAL), by $\text{NADP}\cdot\text{H}_2$ with the aid of a molecule of ATP. Thus, it is at this point that the products of the light phase enter into the reduction of carbon dioxide. PGAL is now at the reduction level of a carbohydrate which corresponds to that of an aldehyde, and it may travel any of several different pathways. It may undergo a series of reactions and eventually be transformed to RDP, it may become modified into glycerol, or it may undergo condensation to form the six-carbon sugar fructose diphosphate, which can undergo dephosphorylation and certain internal transformations to become glucose. Glucose may then serve as a building block for such disaccharide sugars as sucrose or such polysaccharides as starch.

Although PGAL might justly be considered the end product of photosynthesis, PGA is frequently involved in transformations. It may proceed along a pathway leading to the formation of amino acids, which subsequently become involved in protein synthesis, or it may become involved in the formation of fatty acids, which join with glycerol in the formation of fats. Figure 6.7 depicts some of the major pathways which are associated with the dark phase of photosynthesis. Notice that this scheme shows the entrance of carbon dioxide and the products of the light phase (ATP and $\text{NADP}\cdot\text{H}_2$) into a cycle involving the compounds we have discussed. Although we have mentioned only a few of the many possible synthetic pathways taken by PGA and PGAL, it should be obvious that the basic organic molecules which serve as nutrient materials for cells of green plants themselves and for the cells of other organisms are produced in photosynthesis.

In summary, photosynthesis is an extremely complex process, involving many separate reactions. Like virtually all reactions which occur within living systems, they are catalyzed by a complex of specific enzymes. Although the light and dark phases of photosynthesis can be separated experimentally, they are closely interrelated in the overall metabolism of any given photosynthetic cell. In addition to photosynthesis, the plant cell carries on respiration, during

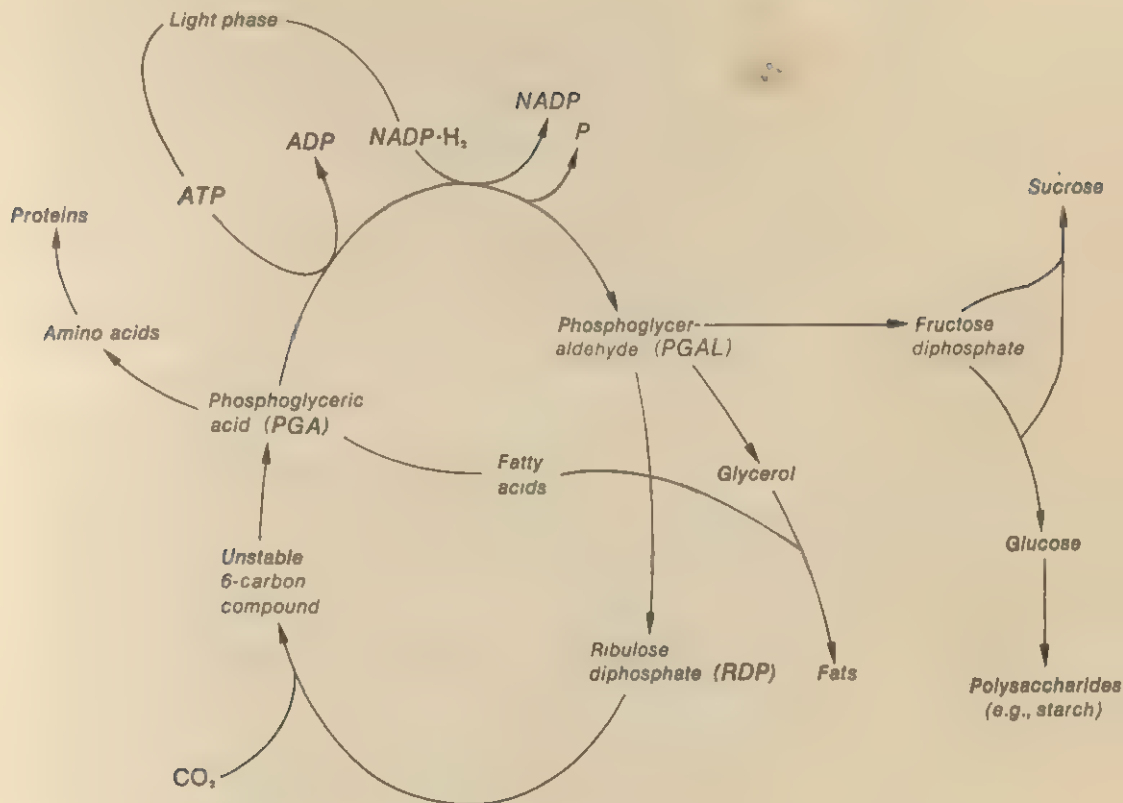


Figure 6.7 Schematic drawing showing the events occurring during the dark phase of photosynthesis. See text for amplification.

which large amounts of ATP are formed, and this ATP supplies energy for many of the synthetic reactions we have mentioned. In other words, the ATP formed during the light phase of photosynthesis is not nearly sufficient to drive the many endergonic reactions carried on in the plant. Nevertheless, our original equation is accurate (although grossly oversimplified) as a summary equation, because every endergonic reaction is driven by energy which is ultimately supplied by sunlight.

SYNTHESES COMMON TO ALL CELLS There are numerous compounds not obtained by cells as prefabricated nutrients; rather, they are synthesized within the cells themselves. These are primarily the organic macromolecules (polysaccharides, lipids, proteins, and nucleic acids) which constitute the bulk of cell contents exclusive of water.

The basic structural features of these macromolecules and the nature of their micromolecular building blocks were discussed in Section 2.4. In addition, we have discussed them from time to time in various connections, the nucleic acids, especially, were given close attention in Chapter 5.

In all cells except the photosynthetic cells discussed above, and the chemosynthetic bacterial cells mentioned previously, the raw materials employed in synthetic reactions come from the digestion (hydrolytic breakdown) of prefabricated materials taken into the organism. The energy necessary to drive these endergonic reactions also comes from these prefabricated materials, in their respiration. Let us now turn our attention to this subject.

Respiration As we noted previously, respiration is that aspect of metabolism in which the raw materials supplied in nutrition are degraded, with an accompanying energy release to the cell. We are now in position to understand that this energy is not actually released, rather, it is transferred from low-energy bonds to the high-energy terminal bonds of ATP molecules. Thus, respiration might be redefined as the manufacture of ATP molecules, using organic fuel molecules as an energy source. Since we have already discussed the mechanics and energetics of the transformations $\text{ADP} \rightleftharpoons \text{ATP}$, let us focus our attention upon the sequence of events leading to the transfer of energy from the chemical bonds of nutrient materials into the high-energy phosphate bonds of ATP. All cells considered, the carbohydrate glucose is apparently the most common cellular nutrient, so let us use the catabolism of glucose to illustrate respiration.

The general reaction for the respiration of glucose is shown below:



It should be noted that this summary reaction is the reverse of that for photosynthesis, and like the overall photosynthetic reaction, it represents a vast number of separate reactions. In general, the respiration of glucose can be divided into two phases, the *anaerobic* and the *aerobic*. Anaerobic respiration occurs in the absence of oxygen, whereas aerobic respiration occurs in the presence of oxygen. The aerobic phase of respiration is not observed in some organisms, due to the absence of enzymes necessary to catalyze certain specific reactions. In fact, O_2 is actually poisonous to some cells. Furthermore, because of certain enzymatic differences in cells, the end products of anaerobic respiration may differ somewhat. However, both anaerobic and aerobic respiration of glucose occur in the cells of the more complex plants and animals. There is also a difference with regard to the sites within a cell at which these re-

spective types of respiration occur. Anaerobic respiration occurs in the general cytoplasm, whereas aerobic respiration is restricted to the mitochondria. From an energetic viewpoint, aerobic respiration results in a far greater transfer (release) of energy than anaerobic respiration, as a consequence, ATP production is primarily associated with the aerobic phase.

The first reaction which glucose undergoes in the anaerobic pathway is a phosphorylation, by means of which *glucose-6-phosphate* is produced. This is an endergonic reaction, and in the reaction a molecule of ATP is dephosphorylated to ADP as the high-energy phosphate bond is transferred to glucose. The glucose-6-phosphate undergoes an internal rearrangement by means of which it is transformed to *fructose-6-phosphate*. This compound undergoes an additional phosphorylation, resulting in the formation of *fructose-1, 6-diphosphate*. This is another endergonic reaction involving another ATP molecule. After this, a complex series of reactions occur during which two high-energy phosphate bonds are formed (the phosphate comes from inorganic phosphate), two molecules of NAD are reduced to $\text{NAD}\cdot\text{H}_2$, and the six-carbon fructose-1, 6-diphosphate is split into two three-carbon molecules of *1, 3-diphosphoglyceric acid* (Figure 6.8).

Up to this point, obviously, the sequence of events is endergonic, not exergonic, as we would expect of a catabolic reaction. However, let us note that we have four phosphate groups in our two molecules

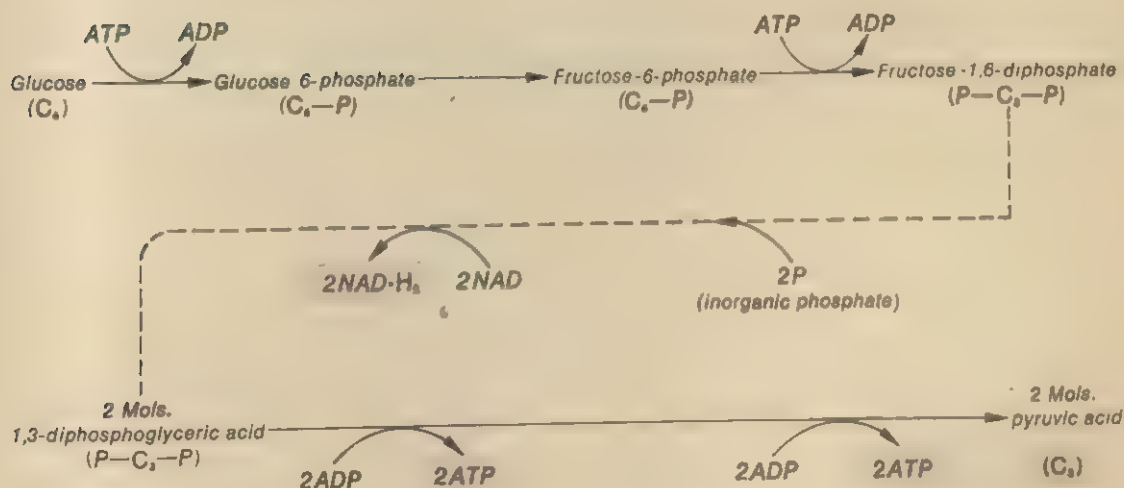
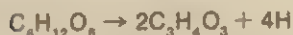


Figure 6.8 Schematic drawing showing the events occurring during glycolysis. End products of the process are shown in color. See text for amplification.

of 1, 3-diphosphoglyceric acid, for which the cell "paid" only two ATP molecules. The other two phosphate groups came from inorganic phosphate. Now the cell is ready to "cash in" on its "investment." By a series of four steps, each molecule of 1, 3-diphosphoglyceric acid is divested of its phosphate groups and transformed into pyruvic acid ($C_3H_4O_3$). During the process, four molecules of ATP are generated, thus returning a net "profit" of two ATP's to the cell (remember, it "spent" two ATP's getting these four). Pyruvic acid is the end product of this sequence of events, which is called the *Embden-Meyerhof* or *glycolytic* sequence. Figure 6.8 shows the sequence of events in glycolysis as we have described them.

Let us note that four atoms of hydrogen are removed from the original glucose molecule in its transformation to pyruvic acid:

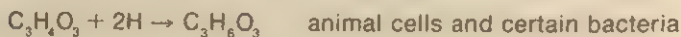


As shown in Figure 6.8, these hydrogens are picked up by two molecules of NAD, which become reduced to $NAD \cdot H_2$. Thus the end products of glycolysis are two molecules of pyruvic acid, two molecules of $NAD \cdot H_2$, and two molecules of ATP.

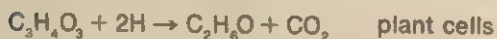
What happens to the hydrogen which was removed from the original glucose and is now held as $NAD \cdot H_2$? It remains in this state until it can be released to molecular oxygen by a series of oxidation-reduction reactions.

This is the usual pathway for hydrogen released in glycolysis, with pyruvic acid being further degraded, and we shall give attention presently to this further aspect of catabolism. First, however, let us see what happens in a cell if the hydrogen produced in glycolysis cannot be given to gaseous oxygen. In most cells, this simply ties up all of the available nucleotide hydrogen acceptor with which it can combine. The damming-up of hydrogen eventually poisons the cell. This explains why most organisms cannot live for very long in the absence of gaseous oxygen. However, there are cells and even organisms that are capable of living in a total absence of oxygen, that is, anaerobically.

Just what do cells existing under anaerobic conditions do with their hydrogen atoms? They simply give them (by way of $NAD \cdot H_2$) to pyruvic acid, forming either *lactic acid* or *ethyl alcohol*:



Pyruvic acid Lactic acid



Pyruvic acid Ethyl alcohol

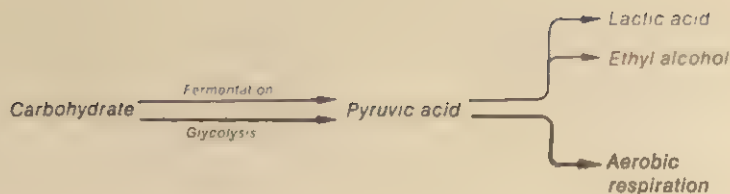
It should be kept in mind that not all cells possess enzymes for making one or the other of these conversions. In fact, relatively few cells can do so. If a cell *does* possess this capability, and hence produces lactic acid or ethyl alcohol under anaerobic conditions, it is said to carry on *fermentation*. If this is the *only* catabolic pathway open to an organism, it is obliged to forego the greater part of the energy which is bound up in carbohydrate molecules and must make up for this by fermenting more carbohydrate if it is to carry on an equivalent degree of metabolism to that which would be possible if it were capable of utilizing oxygen. For example, when yeast cells* are grown under anaerobic conditions, they consume much more carbohydrate in producing a given number of cells than is required under aerobic conditions. To be exact, only about 5 percent of the potential energy in a glucose molecule is made available to a cell in fermentation. Because aerobic respiration is a highly successful adaptation, it is apparently not by accident that the great majority of organisms possess mechanisms which make oxygen utilization possible, since this ability renders a species far more capable of maintaining itself in nature where it is obliged to compete with other species. That there are relatively few anaerobic species is testimony to this principle.

Although the more complex organisms are dependent upon oxygen as a hydrogen acceptor, there are circumstances under which certain cells or tissues may function anaerobically. In muscle cells of man and other vertebrates, for example, energy for contraction is normally provided by the breakdown of ATP to ADP, which is in turn recharged to ATP by a series of steps connected with the complete breakdown of the polysaccharide *glycogen* to carbon dioxide and water. However, under conditions of great activity, the bloodstream cannot supply the muscles with oxygen at a rate sufficient to keep up with hydrogen production, and lactic acid (the end product of fermentation in this case) accumulates. In man, at least, this lactic acid is eventually carried to the liver, where it may be completely oxidized. Under these conditions, therefore, the muscle cells are obliged to function anaerobically, which greatly lowers their efficiency for the time being in terms of glycogen utilization.

As far as man is concerned, the fermentation of carbohydrates by yeasts or bacteria may be turned to his advantage. Ethyl alcohol and lactic acid products have long been valued, and the accumulation of

* Some organisms, such as yeasts, may live either aerobically (utilizing gaseous oxygen as a hydrogen acceptor) or anaerobically (utilizing its own pyruvic acid as a hydrogen acceptor). Others, such as certain bacteria, are said to be *obligately anaerobic* because gaseous oxygen is actually poisonous to them. Most organisms are, of course, *obligate aerobes*.

Figure 6.9 The possible fates of a carbohydrate in catabolism. Note that fermentation and glycolysis are identical processes, except that glycolysis ends with the formation of pyruvic acid and fermentation ends with the formation of either ethyl alcohol or lactic acid.



these substances in the immediate environments of their producers is made possible through their inability to pass their waste hydrogen on to oxygen.

In summary, glycolysis is the anaerobic catabolism of carbohydrates, with pyruvic acid being the end product of the process. Pyruvic acid may then go in either of two directions. If the accumulated hydrogen cannot be given to gaseous oxygen, glycolysis continues as fermentation. If gaseous oxygen is able to combine with hydrogen in the cell, then aerobic respiration of pyruvic acid occurs. These alternate pathways are illustrated in Figure 6.9. We shall now turn our attention to this second possible phase of respiration.

In the presence of molecular oxygen, which serves as the ultimate electron acceptor, a series of oxidation-reduction reactions occur. We have discussed these reactions previously, and at that time, we identified the major molecules involved (nicotinamides, flavins, cytochromes). Our concern here is to emphasize the orderly sequence in which these reactions occur, the role of molecular oxygen in the process, and the energetic considerations which are important to our discussion.

We mentioned previously that the hydrogens removed from the original glucose are held by NAD, which is usually the initial hydrogen acceptor in these oxidation-reduction systems. These systems are referred to alternately as *electron-transport systems*, *hydrogen transport systems*, or *cytochrome oxidase systems*. Cytochrome oxidase (cytochrome a_3) is the terminal acceptor in this chain of organic molecules. The other acceptors are FAD, cytochrome b , cytochrome c , and cytochrome a . Figure 6.10 depicts the sequence of this series and the points at which phosphorylation of ADP to ATP is coupled to the system. As we have shown the series, the oxidized forms of the molecules are at the bottom and the reduced forms are at the top. In the case of NAD and FAD, entire hydrogen atoms are transferred. However, ionization occurs with the oxidation of $\text{FAD} \cdot \text{H}_2$ by cytochrome b , with the result that the cytochromes transfer only electrons. The hydrogen ions are set free within the mitochondrion. At the end of the sequence, when cytochrome a_3 is oxidized, an atom of oxygen joins two electrons and two hydrogen ions, as a result of

which oxygen is reduced to water. As the electrons are passed along the system there are electron shifts in the carriers involved at the points indicated in Figure 6.10, so that electrons pass into lower energy orbitals. As a result, energy is made available, and is incorporated into high-energy phosphate bonds, that is, ADP is phosphorylated to ATP. Thus, a part of the energy released by the respiration of glucose is conserved, although some is dissipated as heat. As we have indicated, all or almost all of the energy would be lost if a given molecule were "shattered" in a single reaction. As it is, the gradual transformation of energy into phosphate bonds by way of the sequence we have outlined constitutes a highly efficient mechanism within the cell.

Now let us consider the two pyruvic acid molecules which result from the glycolysis of a single glucose molecule. In aerobic respiration, you will recall, they are eventually oxidized to carbon dioxide and water. This involves a complex series of reactions, and begins with the passage of pyruvic acid into the mitochondria. Here, a given molecule of pyruvic acid is decarboxylated, and the remainder of the molecule is joined to a molecule of a substance called *coenzyme A* (abbreviated Co-A). The resulting compound, now containing only two carbon atoms of the original pyruvic acid, is called *acetyl Co-A*. The transformation of pyruvic acid to acetyl Co-A also involves a dehydrogenation, that is, two hydrogens are removed from each

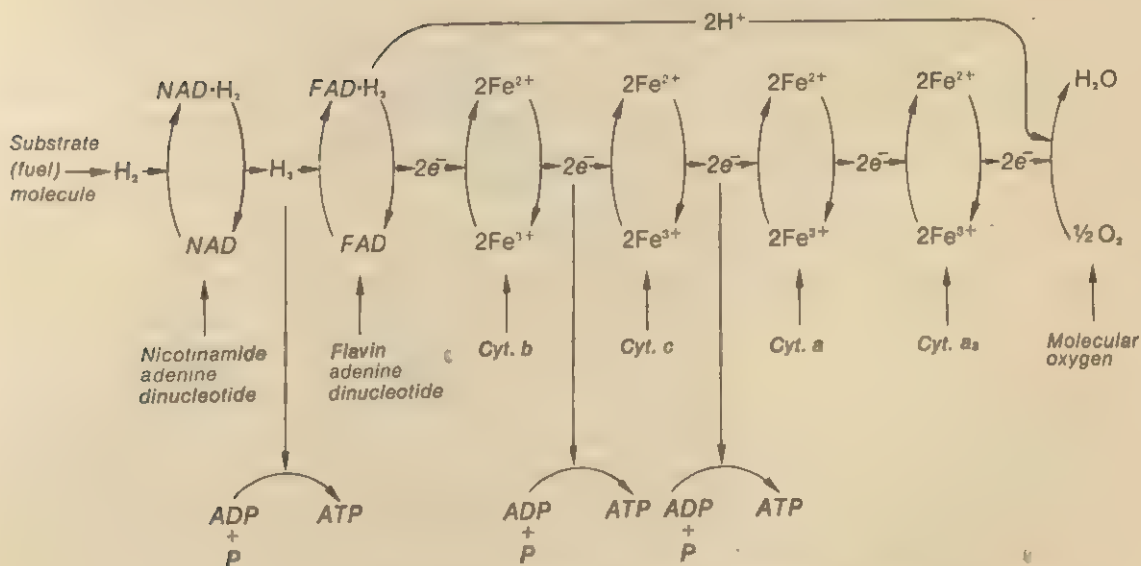


Figure 6.10 Schematic drawing of the cytochrome oxidase system. See text for amplification.

molecule. Thus, two more electrons are available for transfer along the cytochrome oxidase system, which means that three more molecules of ATP are formed for each molecule of pyruvic acid. This transformation, involving what is left of the original glucose molecule, may be illustrated in a highly abbreviated form as follows:



Each molecule of acetyl Co-A now enters a complex series of reactions which constitute a cycle. This cycle is called the *Krebs cycle* in honor of the biochemist H. A. Krebs, who worked out a major part of it, for which he was awarded the Nobel prize in medicine in 1953. It is also called the *citric acid cycle* because citric acid is usually considered the starting point in the cycle. This cycle is a common meeting point for all organic molecules which are utilized by the cell as fuel. It also furnishes carbon skeletons for a number of synthetic metabolic pathways. Since the series of reactions involved form a cycle, we can speak of a starting point in the cycle relative to the point at which it is entered by a given compound, and of an endpoint or product relative to the point just preceding the point of entry. In this context, acetyl Co-A enters the cycle by joining a four-carbon compound called *oxaloacetic acid*, which represents the endpoint of the cycle in this case, to form the six-carbon citric acid, which represents the starting point of the cycle. In the reaction leading to the formation of citric acid from the union of acetyl Co-A with oxaloacetic acid, the Co-A is released and may combine with more pyruvic acid coming into the cycle.

The major reactions which occur in the Krebs cycle, from our viewpoint, are decarboxylations and dehydrogenations. All of the other reactions are simply preparatory to more decarboxylation and dehydrogenation. As a result of decarboxylation, the two remaining carbon atoms of the original pyruvic acid molecule are released as carbon dioxide, and as a result of dehydrogenation, the three remaining hydrogen atoms are passed along hydrogen transfer systems. This latter process, of course, leads to the generation of ATP. Since the original glucose molecule is represented by two molecules of pyruvic acid, two molecules of acetyl Co-A, and so on, this means that *four* atoms of carbon are released as CO_2 in the Krebs cycle, and six atoms of hydrogen are available for transfer to molecular oxygen. However, there is a net addition of three molecules of water to the Krebs cycle for each molecule of acetyl Co-A and this makes twelve additional hydrogens available for every two turns of the cycle. In all, then, twenty-four electrons are delivered to the cytochrome system for each one of the glucose molecules that undergoes complete respiration.

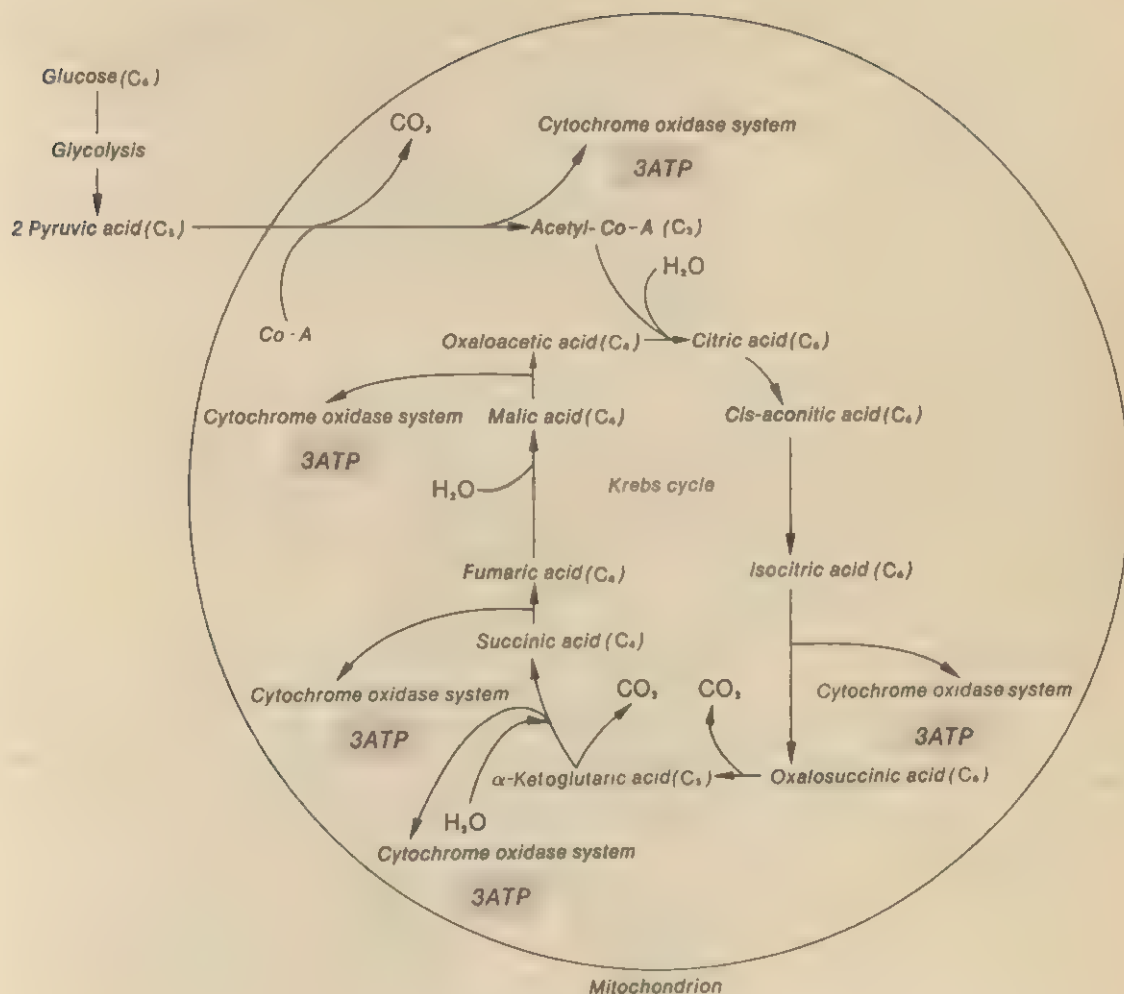


Figure 6.11 Schematic drawing showing the events occurring in the mitochondrion as a part of respiration. Most of these events are a part of the Krebs cycle. Note the points at which hydrogens are removed. ATP yields (colored) are expressed per molecule of pyruvic acid

Figure 6.11 shows the fate of pyruvic acid after it enters a mitochondrion. The major compounds of the Krebs cycle are shown, as well as the points in the cycle at which decarboxylation and dehydrogenation occur. The decarboxylations are represented in the diagram by the release of carbon dioxide and the dehydrogenations are represented by the cytochrome oxidase systems, as indicated. It should be pointed out that Figure 6.11 is oversimplified; the reac-

tions involved are rather complex, and we shall attempt to gain only an overall grasp of their significance. It should also be pointed out that each reaction in the cycle must be catalyzed by a specific enzyme.

With the passage of two molecules of pyruvic acid through the Krebs cycle, the respiration of a glucose molecule is completed. The end products, as shown in our overall equation, are carbon dioxide, water, and energy (in the form of ATP). Let us summarize the energy transformations which occur in the entire sequence by means of the following calculation:

Glycolysis (4ATP - 2ATP)		2ATP
4H	$\xrightarrow{\text{Cytochrome system}}$ 2H ₂ O (from glycolysis)	6
4H	$\xrightarrow{\text{Cytochrome system}}$ 2H ₂ O (from pyruvic acid)	6
4H	$\xrightarrow{\text{Cytochrome system}}$ 2H ₂ O (from isocitric acid)	6
4H	$\xrightarrow{\text{Cytochrome system}}$ 2H ₂ O (from α -ketoglutaric acid)	6
4H	$\xrightarrow{\text{Cytochrome system}}$ 2H ₂ O (from succinic acid)	6
4H	$\xrightarrow{\text{Cytochrome system}}$ 2H ₂ O (from malic acid)	6
Total:		38ATP

How efficient is the cell in conserving the energy contained in a molecule of glucose? If one considers that a gram-molecular weight of glucose contains about 690,000 calories of energy and that one high-energy phosphate bond contains about 10,000 calories, the cell has conserved about 55 percent of the energy (380,000/690,000). Thermodynamically, this is a very high yield, and the cell is thus supplied with a form of chemical energy (the high-energy terminal bond of ATP) with which to drive endergonic reactions, transport molecules across cell membranes, accomplish ciliary movement, and so on. However, as ATP is changed back to ADP with the expenditure of high-energy phosphate bonds, there is further loss in efficiency, and in terms of useful activity, most cells probably realize far less than 55 percent efficiency from their organic fuels.

6.2 Metabolism at the organismic level To a great degree, the metabolism of a multicellular organism is simply the sum of its cellular metabolism. For example, photosynthesis and respiration occur in the individual leaf cells of a tree, and the total activity of the organism with respect to these processes is a function of the number of cells so engaged. Again, if ATP is being generated in the complete catabolism of glucose within one cell of a complex animal body, a similar involvement on the part of other cells only adds to total ATP production. Nevertheless, the metabolism of a complex organism is more than the sum total of its cellular activities.

We can best conceive of metabolism at this level as an emergent characteristic which reflects the high degree of coordination among tissues, organs, and organ systems.

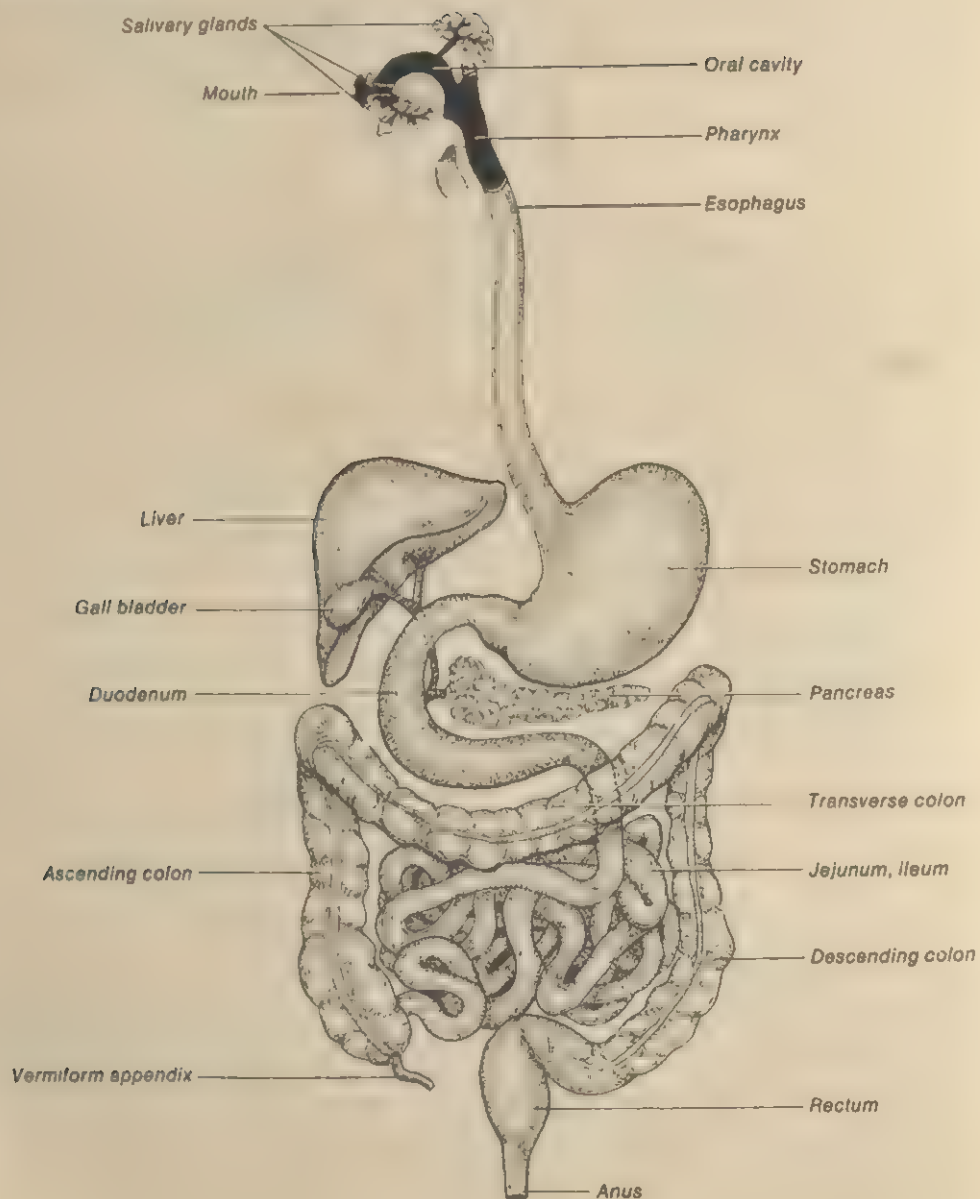
In an attempt to exemplify metabolism at the organismic level, we shall consider separate cases of a complex animal and a complex plant. Since we can assume some familiarity with the structure and function of the human body, and because we have a natural interest in our own metabolic processes, we shall devote some attention to human metabolism. After this, we shall consider the metabolism of a generalized seed plant.

Metabolism of the human body. **NUTRITION.** As one of the animals that possess a tube-within-a-tube body plan, man exhibits a gastrointestinal tract beginning with a mouth and ending with an anus. During embryonic development, the tract grows in length at a more rapid rate than does the body wall, which causes it to be thrown into folds. In a mature human being, it averages about thirty feet in length. Certain accessory organs of digestion, the *salivary glands*, *liver*, *gall bladder*, and *pancreas*, develop as outpushings from the embryonic tract, and when fully developed they lie in close proximity to it. The digestive tube itself consists of the cavity just posterior to the mouth (properly called the *oral cavity*), the *pharynx*, *esophagus*, *stomach*, *small intestine* (consisting of the *duodenum*, *jejunum*, and *ileum*, in that order), and the *large intestine*. Figure 6.12 shows the relationship of these organs to one another.

Food enters the mouth, and any solid portions are retained within the oral cavity for a time, where the teeth render them more susceptible to the chemical action which follows by dividing them into smaller pieces. Simultaneously, the secretion of the salivary glands moistens the food mass, making passage along the esophagus possible, and an enzyme *salivary amylase*, begins a process of hydrolysis whereby the polysaccharide carbohydrates glycogen and starch, if present, are broken down to the disaccharide maltose. Fats and proteins are not chemically affected in the oral cavity.

By the act of swallowing, the moistened food passes through the pharynx and esophagus, entering the stomach through a muscle-enclosed opening. Here it encounters an acid environment, due to the presence of hydrochloric acid in the *gastric juice* secreted by tiny glands in the stomach wall. The salivary amylase, which is inactivated by acid, continues to hydrolyze starch or glycogen for a time, however, because penetration of the food mass by the acid is not instantaneous. Although the gastric juice contains no enzymes capable of acting on carbohydrates, a degree of hydrolysis occurs through the action of hydrochloric acid on some of the bonds that link monosaccharide units together. It appears that very little diges-

Figure 6.12 *The human gastro-intestinal tract and its associated organs. For illustrative purposes, the several organs of this system are somewhat separated from each other. In their normal positions, they are much more intimately associated.*



tion of fats occurs in the stomach, although they are softened. Protein digestion begins in the stomach through the action of *pepsin*, an enzyme present in gastric juice which acts specifically on certain bonds within protein molecules, thus hydrolyzing many of them to shorter chains.

Whenever a quantity of food is present in the stomach, liquefied portions are released at intervals into the duodenum through an opening similar to the one between the esophagus and the stomach. There is usually sufficient alkalinity in the secretions that collect in the small intestine to counteract the acid nature of the liquified food as it comes from the stomach, thus rendering it near the point of neutrality in reaction. It is in the small intestine that the major portion of digestion occurs, the stomach having served chiefly as a site of storage. Secretions from the pancreas and the liver enter the duodenum (Figure 6.13). Small glands located within the intestinal wall secrete enzymes also. As a result of pancreatic and intestinal secre-

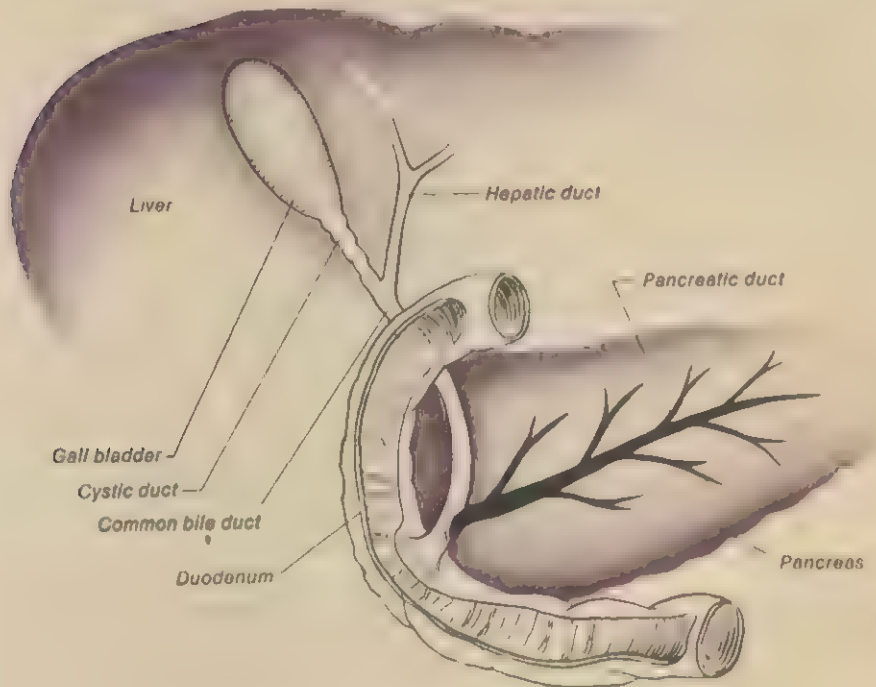


Figure 6.13 The relationship of the liver, gall bladder, pancreas, and duodenum. Bile, produced in the liver, is stored in the gall bladder. It and the pancreatic secretion enter the duodenum at the same point.

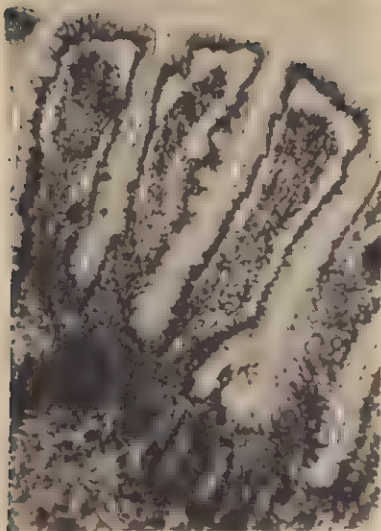


Figure 6.14 Section of human ileum, showing several villi. Note the extent to which the intestinal surface is increased by their presence. Magnification: about 650 times.

tion, the food mass is exposed to a large number of enzymes in the small intestine, each of which is rather specific for certain types of chemical bonds.

Molecules of starch or glycogen which escaped the action of salivary amylase are hydrolyzed to maltose by an amylase secreted by the pancreas. Maltose and other undigested disaccharides are split into their component monosaccharides by enzymes which form a part of the intestinal secretion. Carbohydrate digestion is completed with the production of monosaccharides, which can be absorbed.

It will be recalled that virtually no digestion of fats occurs prior to the time that these enter the small intestine. At this point, however, *lipases* of the pancreatic and intestinal secretions hydrolyze some of the fat molecules to glycerol and fatty acids, both of which can be absorbed. Perhaps more than half of the fat is not hydrolyzed but is finely emulsified to molecular aggregates called *chylomicrons*, which eventually pass through the membranes of the cells lining the inner lumen of the intestine.* It appears that this emulsification is made possible by the combined action of bile salts, found in the secretion of the liver which empties into the duodenum, and the products of fat digestion resulting from the action of lipases. Thus, the first step in the breakdown of fats is the hydrolytic production of glycerol and fatty acids, which then proceed to emulsify the remaining fat with the help of the bile salts.

By the time proteins reach the small intestine, hydrolysis has occurred to an extent through the action of pepsin. The pancreatic enzymes *trypsin* and *chymotrypsin* render the protein chains still shorter by acting upon links for which they are specific, with the result that *peptides* consisting of relatively few amino acids are produced. Various peptidases (enzymes) of pancreatic and intestinal origin then remove amino acids one at a time, and digestion of proteins is completed since amino acids are able to penetrate the cell membranes of the intestinal lining.

Monosaccharides, fatty acids, glycerol, chylomicrons, and amino acids are absorbed into the cells that line the inner surface of the small intestine and pass on to still deeper cells. Eventually, they reach small blood capillaries and lymph vessels which transport them from the intestine. Some of the absorption can be accounted for by simple diffusion, but it is known that under certain conditions active absorption against concentration gradients occurs. The small intestine is well adapted to the process; not only is there a great deal

* Ordinarily, molecules as large as those of fats, to say nothing of several such molecules in aggregate, do not penetrate cell membranes. However, due to the constitution of the plasma membrane (largely fatty materials) such aggregates seem to "squeeze" themselves in by combining with other fatty materials in the membrane.

of surface by virtue of its considerable length (about twenty feet), but the lining is characterized by the presence of folds and by finger-like projections known as *villi* (Figure 6.14), an arrangement which offers a tremendous amount of surface to the digested food.

In addition to its intake of carbohydrates, fats, and proteins, the body requires certain inorganic salts whose ions perform a regulatory function in cellular metabolism, and these must be included in the diet. Certain vitamins are essential to the normal functioning of the body, and in a balanced diet, these are usually present in abundance. Finally, a quantity of water must be received in order to serve the many functions to which this substance is put in the body. Water, vitamins, and inorganic salts require no digestion because their molecules pass through the intestinal lining quite readily.

At this point, let us digress from our main stream of thought and consider more fully the *circulatory* system of man. Early in embryonic life, a *heart* and *blood vessels* form, connect, and in time become functional. At birth (although circulation has already been going on for some months) the system is capable of serving a food-ingesting body. The four-chambered heart (Figure 6.15) is so organized that its two upper chambers serve as receiving stations, and its two lower ones pump blood outward. Two types of vessels attach to the heart: those which convey blood away from the heart are called *arteries*, and those which conduct blood to the heart are called *veins*. The large arteries, in coursing away from the heart, branch into

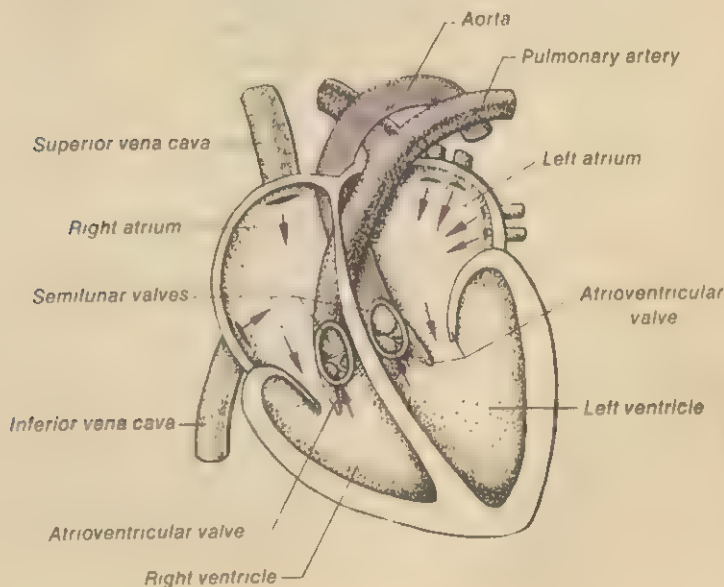


Figure 6.15 Diagrammatic representation of the human heart in frontal section, as it would be viewed from the ventral surface of the body. In its cycle of contraction, the two atria force blood simultaneously into the two ventricles, the wave of contraction spreads downward, and the two ventricles force blood through the pulmonary artery and the aorta at the same time.

smaller and smaller vessels and eventually end in the tissues as *capillaries*, which are of microscopic size. As far as the diffusion of food molecules, gases and wastes are concerned, the capillaries constitute the functional portion of the blood vascular system since their walls are very thin. Ultimately, the capillaries join in a pattern opposite to their original branching, and form the veins.

In its flow through the heart, blood is returned from the tissues through two large veins that enter the *right atrium*. From this chamber, it passes to the *right ventricle* through a valve and is then pumped through the *pulmonary artery* to the lungs. After coursing through the capillary network there, it returns to the *left atrium* by way of two *pulmonary veins*, each of which branches into two veins before reaching the heart, and continues through a valve into the *left ventricle*. From here, it is pumped through the *aorta*, the largest artery in the body, to the many branch vessels of the arterial system. After passing through the capillary network, it returns to the heart by way of the venous system (Figure 6.16). Although the velocity of blood flow varies with a number of factors, including degree of physical activity, a given blood cell completes this cycle, on the average, in a little over a minute's time.

Distinct from the blood-vascular system, but a vital part of circulation, is the lymphatic system. The vessels of this system branch into capillaries, but unlike those of the blood-vascular system, they do not connect with others but simply end in the tissues (Figure 6.17). They play an important part in returning fluids from the tissues (a result of filtration, diffusion, and osmosis outward from the blood-vascular capillaries) to the main circulatory system. Eventually, the *lymph*, as tissue fluid is called after its collection in these capillaries, is carried to certain large veins near the heart, chiefly through two main lymphatic vessels.

Regarding the digestive process, the small intestine is richly vascularized by capillaries which merge to form veins, and these in turn eventually form one vessel, the *hepatic portal vein* (Figure 6.16). This vessel conducts blood from the intestine to the liver, where it branches into smaller and smaller vessels until capillaries are again formed. Thus any products of digestion reaching the intestinal capillaries are carried to the liver. This is the course taken by monosaccharides and amino acids. Although it appears that fatty acid molecules which are relatively small largely follow this same route, the usual pathway taken by products of fat digestion is that provided by capillaries of the lymphatic system, whose main ducts eventually empty into the blood stream. Hence, these products reach the main circulation without going to the liver as do monosaccharides and amino acids.

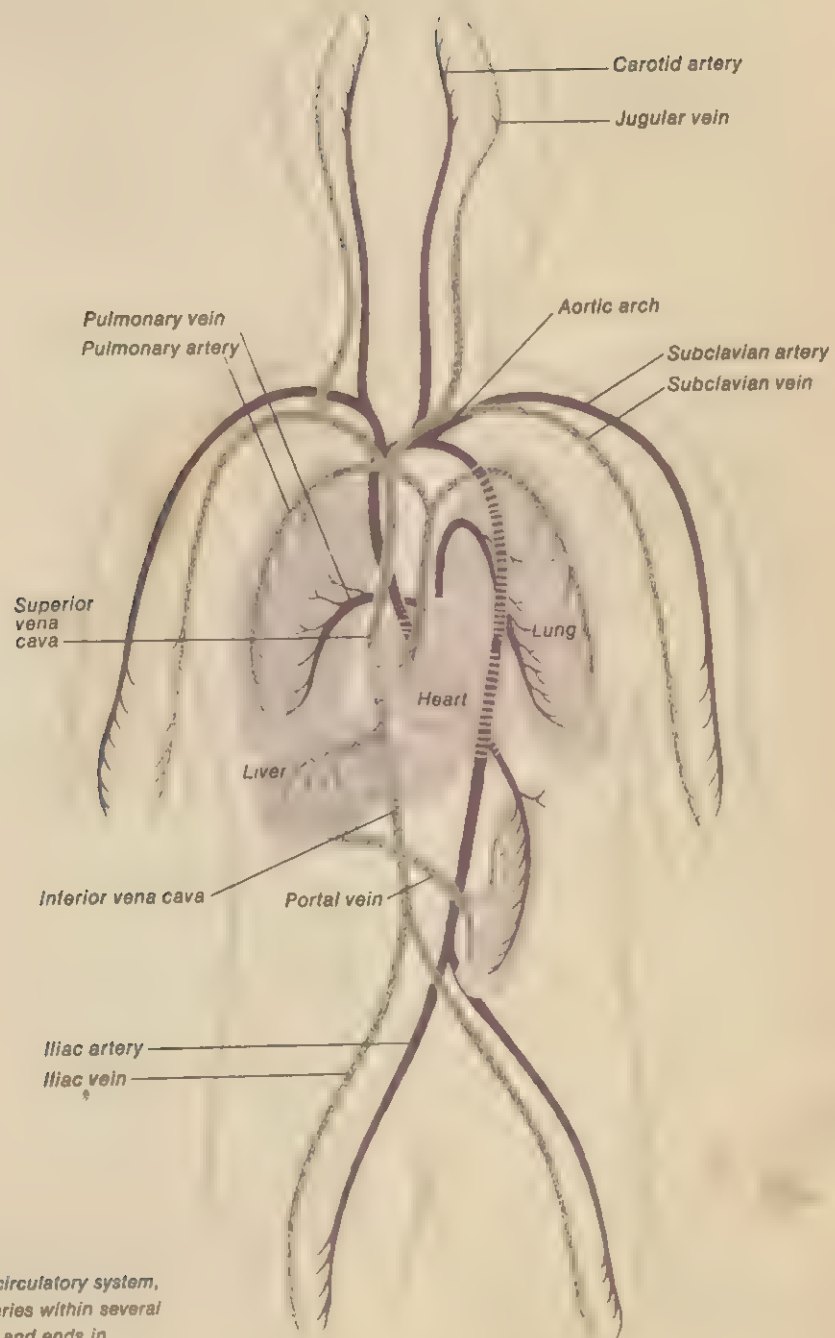


Figure 6.16 Simplified diagram of the human circulatory system, showing the relationship between veins and arteries within several organs. Note that the hepatic portal vein begins and ends in capillaries.



Figure 6.17 A comparison of blood capillaries, which form a continuous network, with lymphatic capillaries, which are "blind." Notice that both are closely associated with cells.

SYNTHESIS The chief function of digested carbohydrates is that of furnishing the body with a ready source of energy, and the blood stream maintains a fairly constant level of glucose under normal dietary conditions. If this level has fallen during a period of fasting or starvation, glucose and other monosaccharides received from the small intestine are picked up directly from the liver without alteration and are carried to the tissues. Under normal circumstances, however, they are converted in the liver to glycogen and are stored by the liver in this form. Liver glycogen may be built up to a point of saturation, and excess glucose is then converted to fat in certain tissues of the body. Although the liver is the central "bank" for glycogen in the body, this substance may be maintained to some extent in "branch banks" such as muscles. Once glycogen is formed in the liver, however, it must be hydrolyzed to glucose before it can be transported to other tissues, where a reverse process (dehydration) results in its re-formation into glycogen.

Under normal conditions, it appears that glycerol, fatty acids, and chylomicrons travel directly from the intestine to sites of storage called *fat depots*, of which the mesenteries and the tissues just beneath the skin are most important. Glycerol and fatty acids are recombined into fats which, together with the chylomicrons, serve as raw materials for the synthesis of the particular type of fat characteristic of the human species. Whenever the energy requirement of the body is such that carbohydrate intake is insufficient to meet it and to maintain a normal level of glycogen in the liver and other tissues,

these fat stores are called upon. It appears that they are transported under these conditions to the liver, where they are split to glycerol and fatty acids, which then become available to the cells of the body.

Although carbohydrates and fats are involved to a certain extent in anabolic processes within cells, they function primarily as sources of energy for the body. In the case of proteins, the reverse is true. The primary function of amino acids as they are absorbed from the intestine is that of protein synthesis, and it is through this process that cells build up their enzymes and structural proteins. After these requirements are met, excess amino acids are converted in the liver to other readily utilizable substances. There is virtually no storage of proteins and amino acids in the body, and these substances must be taken into the body at fairly frequent intervals. If the supply of amino acids is inadequate, the body eventually meets its requirements by utilizing certain of its own tissues. Under conditions of a normal diet, however, the intake of protein is somewhat greater than that necessary to maintain the tissues. This results in an excess of amino acids in terms of their primary function, and it is these units which enter into transformations in the liver. The conversion of amino acids to other substances or their entrance into the citric acid cycle involves the loss of their NH_2 groups, which are eventually excreted as urea.

In spite of the inability of the body to build up amino acids from fats and carbohydrates alone, since these substances possess no nitrogen, a certain amount of amino acid synthesis takes place. Some are formed through modification of others, and some are produced from nonprotein materials. Certain of the amino acids, however, cannot be made; these must be included in the diet, hence they are termed *essential amino acids*. Eight of the twenty amino acids which make up the proteins of the human body are essential to man. Not only must these be included in the diet, but they must be present in amounts sufficient to meet the anabolic requirements of the body. It is therefore possible that the body may receive amounts of protein which are more than adequate in a quantitative sense, but if there is a deficiency in even one essential amino acid, the result is a break in the nutritional chain. Fortunately, most proteins are complete in their inclusion of essential amino acids, although not all are equally rich in them. In general, proteins of animal origin are richer than those of plants in this respect, which means that the daily intake of protein must be larger when plant products are chiefly or exclusively utilized as a source.

With the build-up of fat, glycogen, and blood glucose, the body is equipped with immediate and reserve fuels with which to stoke the catabolic fires. Respiration is made possible in the cells through the

passage of hydrogen to gaseous oxygen, this final acceptor being transported to the cells by way of the blood stream in loose chemical combination with *hemoglobin*, a pigment present in red blood cells. In addition to a catabolic function, glucose and certain types of fat molecules may also enter into anabolic reactions of various sorts. Growth, repair, and maintenance are made possible by the absorption of amino acids from the blood stream into cells, and any surplus of these is diverted to the function of energy production through loss of their nitrogen in the liver.

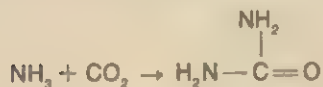
Although most of the vitamins which are required by the human body are a part of the normal diet, two vitamins, D and K, are synthesized in quantity within the human body. The action of sunlight on a substance in the skin called *ergosterol* changes it to Vitamin D, and bacteria of the intestinal tract manufacture vitamin K, which is absorbed when their cells disintegrate. Apparently, no other vitamins are manufactured by the body or obtained from bacterial synthesis in the intestine, at least in appreciable quantities.

In addition to the synthesis of carbohydrates, fats, proteins, and certain vitamins, a variety of other compounds are formed. Among these are nucleic acids, complex lipids, and hormones. The complexity of these synthetic reactions is such that we shall not attempt to enter into this aspect of metabolism, but suffice it to say that the production of new cells alone involves the synthesis of a myriad of compounds. Furthermore, the functioning of the human body involves many complex substances, such as hormones, and the total synthesis and utilization of such compounds are delicately balanced within a homeostatic system of grand proportions. We have already seen how isolated parts of this system work as steady-state mechanisms, but as we have pointed out, homeostasis at the organismic level involves a coordination of such mechanisms. Nowhere is this more clearly emphasized than in the synthetic reactions of the human body.

There is one additional aspect of synthesis which deserves some attention, and that is the formation of compounds which eventually leave the body as waste material. Here again, these synthetic reactions are an important part of homeostasis. Since the formation and elimination of these compounds involve special organ systems, we shall consider this aspect of synthesis in some detail.

Excluding digestive residues from consideration, the two major classes of waste products of the human body are carbon dioxide and a wide variety of nitrogenous materials. The elimination of carbon dioxide involves a rather simple transformation, but it is so closely identified with respiration that we shall discuss its elimination in the next topic of this section. With regard to the nitrogenous wastes, two

organs are chiefly involved: the liver and kidneys. The liver is a metabolic jack-of-all-trades whose cells become involved in the most complicated catabolic and anabolic reactions which occur in the human body. Its important role in metabolism is reflected by its size and by its close relation to all other organ systems via the circulatory system. Most of the degraded (and in many cases, resynthesized) compounds in the liver eventually form a part of the bile, which is stored in the gall bladder and released into the duodenum at intervals. Bile consists of these compounds, assorted materials such as the pigment hemoglobin from degenerating red blood cells, which are broken down in the liver, and a quantity of inorganic salts. We have already noted that these salts play a part in the digestion of fats in the small intestine. Bile is eventually eliminated from the body in the feces, and by this means, the body gets rid of a whole host of nitrogenous materials whose continued presence would otherwise interfere seriously with homeostasis. In addition to the nitrogenous compounds which are eliminated in this fashion, the liver incorporates waste nitrogen into certain other compounds that are released into the blood stream. Eventually, they are filtered out by the kidneys and eliminated in the urine. Quantitatively, the most important member of this class of compounds is urea, which is synthesized from amino groups derived from protein catabolism. The synthesis of urea in the liver is a complex process, but essentially, it involves the conversion of amino ($-\text{NH}_2$) groups to ammonia (NH_3) and the addition of CO_2 to ammonia to form urea:



We have made no attempt to balance this equation; it should not be taken as a direct, quantitative expression of the synthesis of urea. Actually, several compounds are involved in cyclic fashion, and our equation is merely intended to indicate an overall synthetic reaction.

The paired kidneys are located near the dorsal body wall at about the level of the waist. Each is supplied with an artery and a vein, and a urinary duct, the *ureter*, leads from each to the *urinary bladder*. From this site of temporary urine storage, a single tube, the *urethra*, leads to the outside of the body (Figure 6.18).

Functionally, the kidney operates in extracting urea and certain other nitrogenous wastes by means of an intimate relationship between the capillary bed of its blood vessels and the functional units of the kidney, called *nephrons* (Figure 6.19). There are about a million nephrons in each kidney, all of which eventually empty into the pelvis, or collecting space (Figure 6.18). Each nephron consists of

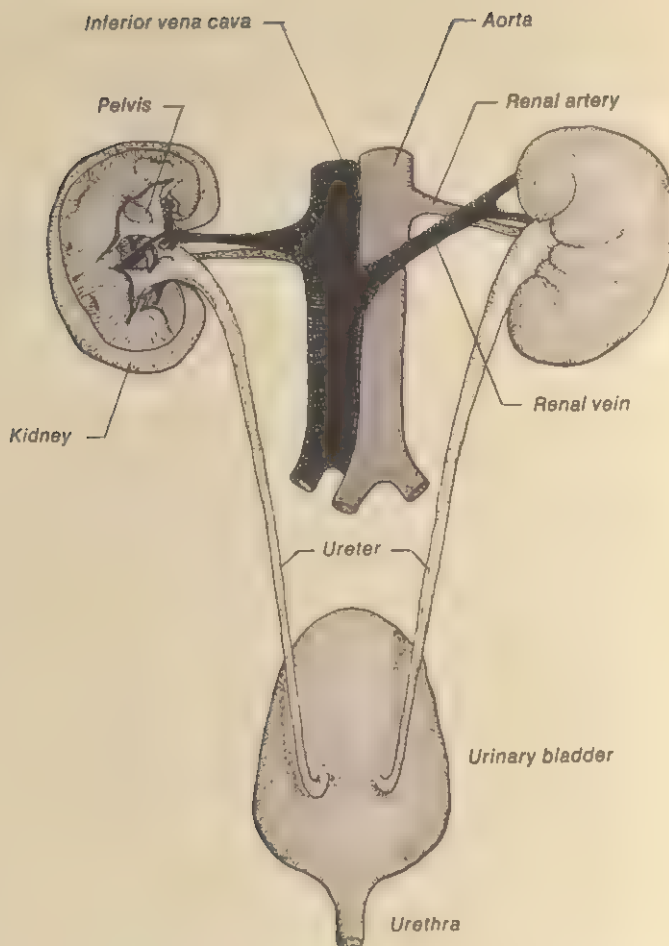


Figure 6.16 The human urinary system, shown with its associated blood vessels.

a capsule, which looks like a cup in cutaway view, and a long tubule, which connects with others to afford a common drainage into the kidney pelvis. The capsule is filled with a tuft of arterial capillaries, and it is here that removal of materials from the bloodstream actually occurs. The walls of both the capillaries and the capsule are extremely thin, and blood pressure causes filtration of materials to occur from the blood stream into the tubule by way of the capsule. How, it might be asked, does the tubule differentiate between waste materials and those in the blood which are of further use to the body? The answer is, it does not. The capsule removes quantities of water, glucose, salts, and other materials. In fact, anything in the blood may filter through except the "formed" materials of the blood (cells and platelets) and the so-called plasma proteins, or normal

proteins of the blood, whose molecules are too large to filter through the plasma membranes of the cells involved. As a result of total filtration in both kidneys, 35 to 40 gallons of fluid are collected in a 24-hour period! Obviously the body cannot spare this much fluid, and we must look for some mechanism whereby some of it is reclaimed. This mechanism resides in the tubules of the nephrons, where a capillary net lies in close proximity to each tubule (Figure 6.19). It is here that most of the water and many of the other materials originally filtered out are reclaimed by the bloodstream through a process of active absorption. Under normal conditions, the kidneys retain only urea, some other waste products, a small quantity of salts, and enough water to produce a total of about a quart and a half of urine within a 24-hour period.

Although bile and urine include most of the waste materials of the human body, there are a few other mechanisms that should be mentioned. The sweat glands, whose major function is that of tem-

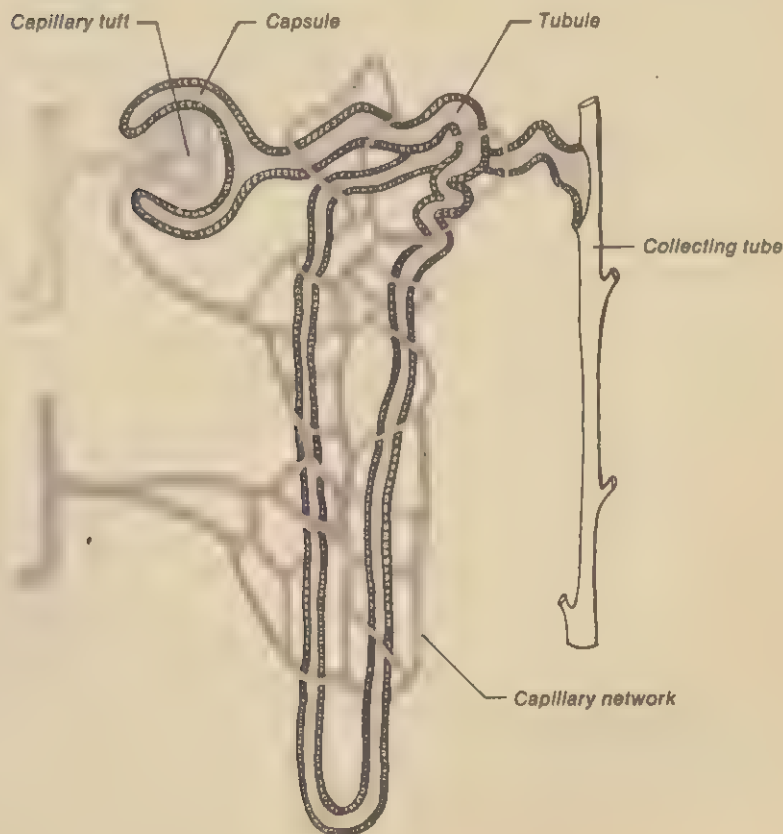


Figure 6.19 A single nephron of the human kidney and its relationship to the blood-vascular system. For purposes of representation, the tubule is made somewhat shorter here than it actually is.

perature regulation, ordinarily remove a little more than a pint of fluid per day from the body. This fluid contains small amounts of urea and other wastes. Many other tissues function in a limited excretory capacity through the production of fluids containing small amounts of waste materials, for example, the linings of the nasal cavities.

RESPIRATION As we have seen, respiration at the cellular level of metabolism involves oxygen as the ultimate electron acceptor. The combination of electrons, hydrogen ions and oxygen results in the formation of water, which is utilized within the cell. At the complex organismic level, respiration is defined as the exchange of gases between an organism and its environment. In the human body, as in most complex animal bodies, this involves *breathing*, by means of which oxygen is brought into the body and carbon dioxide is removed, and internal *transport* of these gases to and from the breathing apparatus. We shall consider these two aspects, or phases, of respiration in turn.

The breathing system of man is so constructed that a pair of lungs occupy the *thoracic cavity*. They are held open or inflated by the below-atmospheric pressure of the cavity. Each lung is supplied with branches of an air-tube, the *bronchus*, and the two bronchi join to form the *trachea*, which opens into the pharynx at the point where the esophagus begins (Figure 6.20). As the *diaphragm* and certain

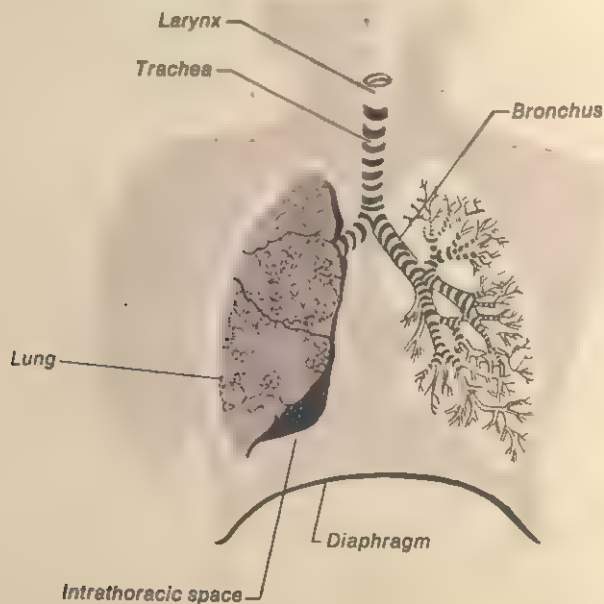


Figure 6.20 A diagram of the human breathing system. Contraction of a broad muscle, the diaphragm, creates a pressure deficit in the intrathoracic space, and air is pulled into the lungs. Relaxation of the diaphragm allows the lungs to partially deflate through their own elasticity. By this means, air is alternately inhaled and exhaled.

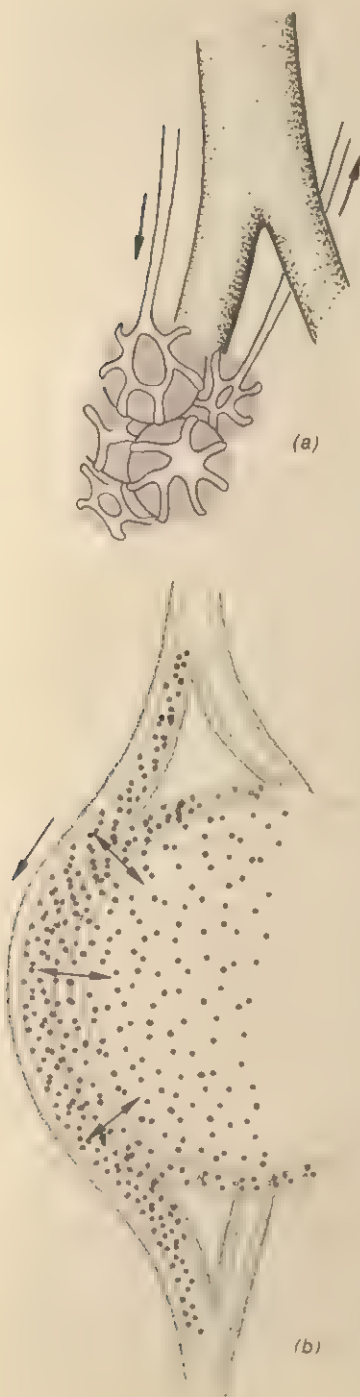


Figure 6.21 Gaseous exchange in the lung. (a) Capillary network surrounding air sacs of the lung. Close proximity of cells enables gaseous exchange to occur. (b) Diagram showing the net diffusion of oxygen (•) from air sac to capillary and that of carbon dioxide (•) in the opposite direction.

muscles of the chest undergo contraction, the thoracic cavity is expanded. Air rushes into the lungs in response to the partial vacuum created by such action, and oxygen is thus made available to the cells of the lungs. Relaxation of the muscles causes the lungs to undergo partial collapse due to their own elasticity, and a quantity of air is expelled.

Functionally, gaseous exchange occurs in the lungs by virtue of the thinness of the lung tissues and of the walls of capillaries which supply them. This exchange is apparently to a great degree a matter of simple diffusion; there is a continual tendency for oxygen to move into the capillaries, and for carbon dioxide to move into the lungs. Intimate contact of cells makes it possible for this exchange to occur (Figure 6.21). As would be expected, inhaled air contains more oxygen and less carbon dioxide than exhaled air. As a matter of fact, the air of the atmosphere, as it is inhaled, contains about 20 percent of oxygen and 0.03 percent of carbon dioxide, whereas exhaled air contains about 16 percent of oxygen and 4 percent of carbon dioxide.

Once in the bloodstream, oxygen combines with the hemoglobin of red blood cells and is transported throughout the body in the form of *oxyhemoglobin*. The bonds which hold oxygen to hemoglobin are very weak ones, and eventually, dissociation of oxyhemoglobin occurs. At this point, hemoglobin may be returned to the lungs for another load, and oxygen makes its way to the individual cells of the body. As we have seen, the capillary network of the blood-circulatory system is widespread in the body, and no cell is very far removed from a capillary. Hence, a constant oxygen supply from the blood stream is assured under normal conditions of body activity. Conversely, carbon dioxide passes from the cells into capillaries, and is thus transported to the lungs. In the case of carbon dioxide, however, hemoglobin is not the chief carrier. For the most part, it combines with water to form carbonic acid, which ionizes in the blood stream to form hydrogen ions and bicarbonate ions:



Carbon dioxide is thus transported through the bloodstream in the form of bicarbonate ions. Eventually, a reversal of this series of reactions releases carbon dioxide to the outside environment by way of the lungs.

The movement of oxygen from the blood stream to the tissues and the movement of carbon dioxide from the tissues to the blood stream are consistent with the so-called gas laws of physics and chemistry, and in essence, this means that these gases are responsive to differential pressures. In other words, if there is less oxygen per volume of space in the tissues than in the bloodstream, dissociation of oxyhemoglobin occurs, and gaseous oxygen moves into the tissues. Conversely, if there is less carbon dioxide per volume of space in the bloodstream than in the tissues, carbon dioxide moves into the bloodstream. Since a continuous oxygen deficit is normally present in the tissues, and a carbon dioxide deficit is the usual condition in the capillary blood, the exchange of gases at the site of the tissues is assured. Similarly, the reverse situation prevails between the capillary network in the lungs and the air within the lung sacs.

Let us note at this point that the blood circulatory system is functional in all three basic aspects of human metabolism (nutrition, synthesis, respiration). This demonstrates the nature of homeostasis in the complex animal body, that is, it is an emergent characteristic rather than a mere sum of individual homeostatic mechanisms. It is true, of course, that an abundance of such individual mechanisms can be demonstrated. For example, in the blood and the fluids which bathe tissues, a complex of buffering compounds maintains a reaction which varies little from a constant pH of 7.33 to 7.38 in the human body. Taken as an isolated case, this is a homeostatic mechanism; if hydrogen ions are suddenly released into the body fluids, they tend to lower the pH, but mechanisms are immediately thrown into action which counteract this tendency. Conversely, the addition of hydroxyl ions is counteracted by other components of the general buffering system. In actual practice, however, this is not an isolated situation which is merely confined within the body fluids. Both the kidneys and the lungs influence pH regulation directly, and ultimately, almost every organ system becomes involved in some way. In the final analysis, then, homeostasis at this level of organization is characteristic of the organism as a whole.

Metabolism of a complex plant In considering plant metabolism, we shall not choose a specific example, inasmuch as our generalizations will be broadly applicable. Indeed, we could have taken this approach in our consideration of the metabolism of a complex animal body. Virtually all that we said there applies to any mammal, and with some exceptions, to any vertebrate. However, in order that we might have a definite starting point, let us consider that we are talking about a seed plant, perhaps a bean or tomato plant or an oak tree.

NUTRITION A seed plant has its beginning in the reproductive processes of a parent plant. Essentially, a seed is a reproductive unit which consists of an embryonic plant and certain associated tissues which are chiefly organic nutrient materials. Under suitable conditions of moisture, temperature, and oxygen availability, the embryonic plant within the seed begins to undergo cellular activity. However, it cannot grow without a source of oxidizable organic molecules, and as yet it does not possess the ability to manufacture any. Under these conditions it produces enzymes which initiate hydrolytic reactions among the surrounding organic nutrients. As a result of this enzymatic activity, organic micromolecules (chiefly glucose from starch digestion) are absorbed into the embryonic plant, where they are utilized in its metabolism (Figure 6.22). In essence, then, an embryonic seed plant starts its metabolic existence as a heterotroph, not as an autotroph.

With continued growth (see Section 7.5), a root system forms. Not only does this provide anchorage for the plant in the soil; water and dissolved mineral substances become available to it, inasmuch as they are transported by the root system to the remainder of the plant body. Meanwhile, a stem with leaves grows upward, penetrates the soil surface, and becomes exposed to air and light. By this time, chlorophyll has developed, and the plant has become independent of

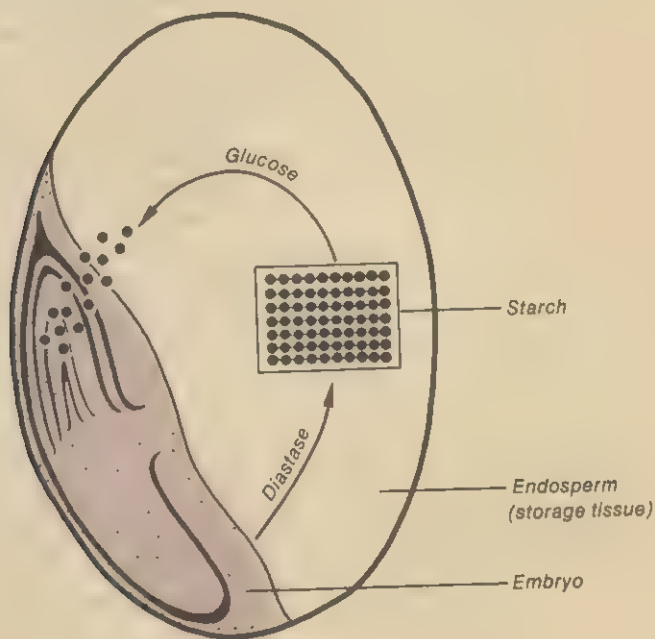


Figure 6.22 Diagram illustrating the digestion of starch in a seed. A hydrolytic enzyme, diastase, is produced within cells of the embryo under proper environmental conditions. This enzyme moves into the endosperm, where it digests starch. The resulting glucose molecules are absorbed into the embryo cells, where they are metabolized.

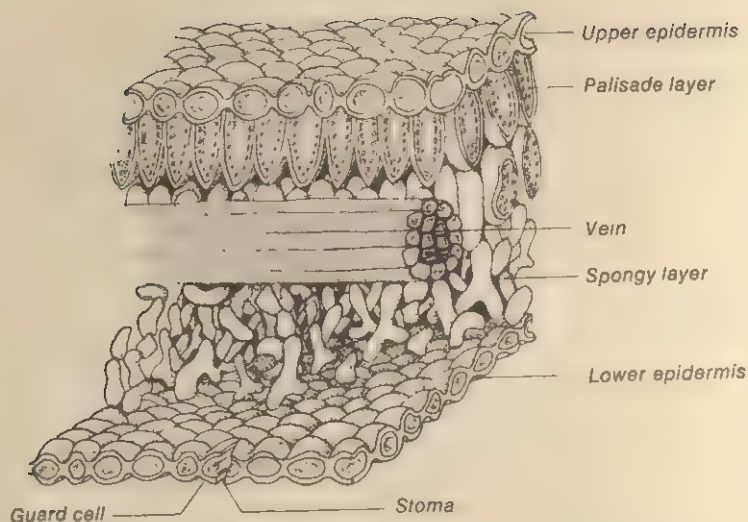


Figure 6.23 Three-dimensional representation of a portion of leaf blade. Note the position of the stoma shown with its guard cells as it relates to the internal tissues.

the organic molecules originally stored in the seed from which it grew. From the point of chlorophyll development until its death, the plant is autotrophic in its nutrition.

The inorganic nutrient substances required by an autotrophic plant are carbon dioxide, oxygen, water, and a variety of mineral substances. Carbon dioxide and oxygen enter the plant through its leaves, and water and minerals enter through its roots. The entrance of carbon dioxide and oxygen into leaves simply involves the diffusion of these substances through the *stomata* of the leaf (Figure 5.11). You will note in Figure 6.23 that the leaf is a layered structure, and that the area immediately adjacent to the lower epidermis, where stomata tend to be concentrated, is composed of cells which do not nearly fill up all of the space. This arrangement makes it possible for atmospheric gases to circulate freely among the cells. Even the more tightly packed cells of the upper (*palisade*) layer have some space between them; thus, all cells of the leaf are in direct contact with oxygen and carbon dioxide. The passage of these gases into and out of cells is consistent with the gas laws which we mentioned in the previous topic.

The transport of water and minerals from the root system to the remainder of the plant is a much more complicated process, and some aspects of it are poorly understood. Probably the best explanation is the *transpiration-cohesion-tension* theory (Figure 6.24). According to this theory, the evaporation of water from cells within the leaf to the atmosphere through the stomata (*transpiration*) creates a water pressure deficit which eventually reaches to the xylem tissues. A continuous column of water exists in these tissues,

and as evaporation occurs from above, tension is placed on the column. Due to the cohesion of water molecules, the column is slowly lifted. Hence the force which causes the rise of water in the plant is held to be the evaporation of water from the leaf with its attending pressure deficit. Although minerals are absorbed into root tissues by forces which are independent of water movement, as soon as they reach xylem tissues they are apparently swept along with the rising column of water. By this means, they reach the leaf cells where they may become involved in synthetic or other metabolic reactions.

SYNTHESIS Although young stems possess chlorophyll and are photosynthetic, the leaf is the major photosynthetic organ of the plant. Since we have already discussed photosynthesis as a cellular phenomenon, we shall simply describe some of its broader aspects at this point. The photosynthetic process yields PGAL and oxygen. Some of the oxygen may be utilized within the cell in respiration (see below), but for the most part, it diffuses from the leaf by way of the stomata. PGAL may be used by the cell in which it is produced, but during active photosynthesis, its production far exceeds the requirements of the cell for organic nutrients. Excess PGAL may then follow any one of three pathways: (1) it may be stored within the cell as starch; (2) it may be combined with minerals in the formation of complex compounds such as chlorophyll; (3) it may be converted to transport carbohydrate (usually the disaccharide sugar sucrose) and secreted to the outside of the cell. In the case of this last alternative, the carbohydrate material moves into the conducting tubes of phloem, which convey it to various parts of the plant. Thus, although simple carbohydrates are the immediate products of photosynthesis, the green plant does not ordinarily build up great quantities of these substances. Rather, they serve as raw material for the further synthesis of organic compounds. They may be converted to more complex carbohydrates or to fats in the plant, or they may be combined with nitrogen and other elements available to the plant in its environment to form proteins. Vitamins, enzymes, and various materials essential to the well-being of the plant may finally be formed by such modification of these carbohydrates, and even more chlorophyll can be synthesized from them. It may be said (metaphorically) that the green plant is a very able chemist, producing a variety of substances from fundamental materials. The actual chemistry of reactions which occur in green plants is extremely complex and is still the subject of much intense research.

There is a common notion that green plants obtain their organic nutrients from the soil, or, in the case of aquatic species such as algae, from the aqueous medium. This is a mistaken idea; as we have seen, the green plant manufactures its organic nutrients from in-

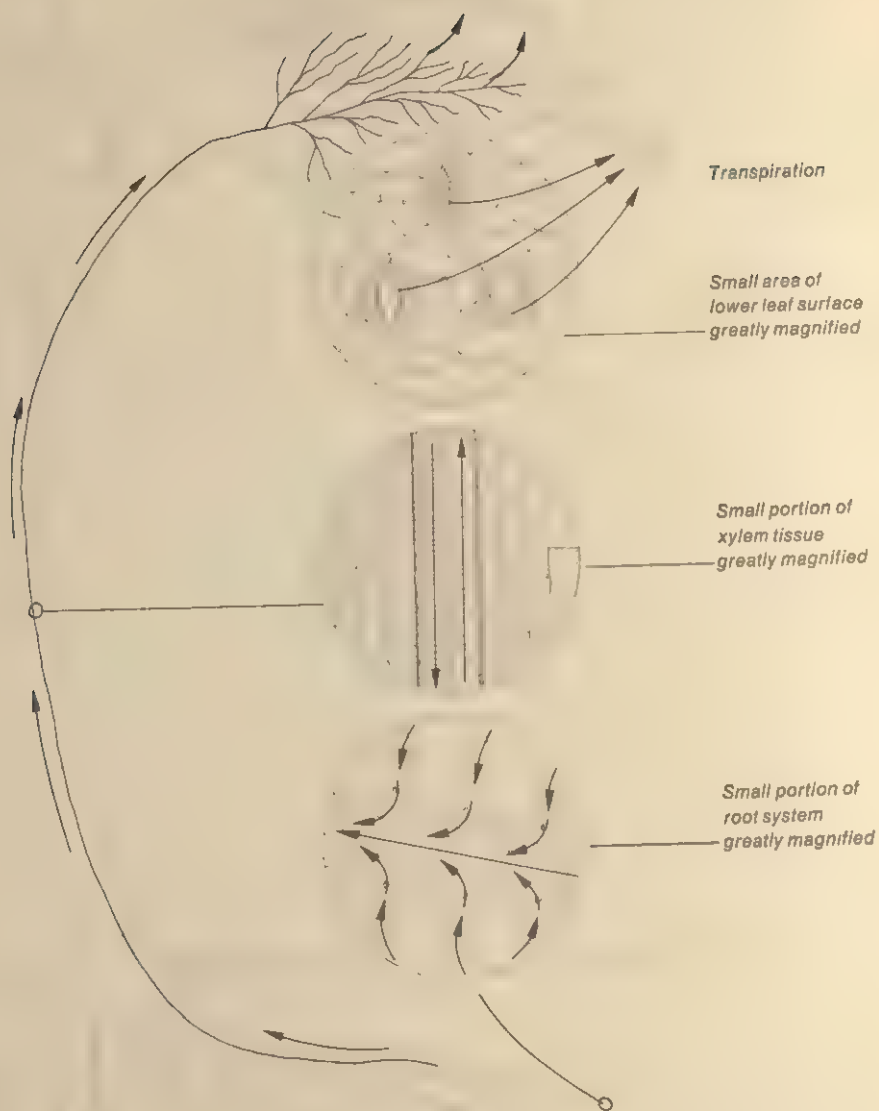


Figure 6.24 *Diagram showing water movement in a plant according to the transpiration-cohesion-tension theory. Water evaporates through stomata, creating a pressure deficit in cells of the leaf. This, in turn, creates a deficit in the xylem of the leaf veins, and eventually water moves up from the roots in response to this deficit. Finally, water is absorbed from the soil by the tiny root hairs. In this manner, water moves upward continuously as long as the stomata are open.*

organic precursors. It is true that these plants depend upon their environments for essential substances such as water, carbon dioxide, and inorganic salts, but these are not energy-yielding compounds. As for plants that grow in the soil, a simple experiment will show that it is not from the soil itself that the substance of a plant is chiefly derived. A container may be filled with dirt, oven-dried, and weighed. If the seed of some plant is inserted into the soil and thoroughly watered, the seed will germinate into a plant. After the plant has grown to a considerable size, it may be pulled up and separated from the soil in which it was growing. If great care has been taken to ensure that all the original soil is still present, and if all plant parts are removed from it, a second drying and weighing will indicate that the soil has lost only an extremely small percentage of its original weight. When the plant is weighed, it will be found that it is many times heavier than the soil which has been lost. Of course, much of the weight of the plant is accounted for by the water it has absorbed. However, even its dry weight will be found to equal many times that lost by the soil. It was experiments such as this that led early plant physiologists to the realization that the body of a land plant derives its mass from some source other than soil. We realize now that synthetic reactions account for this increase in mass, and that the soil (excluding water) furnishes only an infinitesimal portion of the matter which eventually composes the plant body.

Those green plants which exhibit bodies of considerable size and complexity generally produce more organic materials in favorable seasons than they can use, and these may be stored in some form within one of the plant organs. The most common sites of storage are roots (as in sweet potatoes) and stems (as in sugar cane), but the leaves may also serve in this capacity. In seed plants the seeds (and often the fruits, in flowering plants) are sites of considerable deposition of organic nutrients. Under certain circumstances the plant may utilize these resources or, as is more frequently the case, they may serve in the propagation of the species. A seed, for example, is an embryonic plant wrapped in a large quantity of nutrients.

RESPIRATION Because photosynthesis occurs in green plants, there is a prevalent but erroneous belief that respiration occurs only

in animals. Perhaps this idea results from attempts on the part of authors and teachers to simplify metabolism by saying that animals "breathe" oxygen and plants "breathe" carbon dioxide. As is the case with many erroneous ideas, there is some truth to such a viewpoint, since animals *do* consume oxygen from their environments, and plants that are active in photosynthesis exhibit a net intake of carbon dioxide over that of oxygen. However, it should be obvious at this point that whenever a green plant derives energy from a food-stuff it is obliged to utilize oxygen *exactly as an animal does*. This may easily be demonstrated by allowing a number of seeds to germinate within a closed container. It will be found that they deplete the oxygen in the atmosphere of their container within a short time and will stop growing until they are supplied with more. Another way of showing this is to measure gaseous exchange in a green plant which is maintained for a time in darkness. Under these conditions, it will be found that oxygen is utilized, and carbon dioxide is produced.

Nevertheless, in its overall metabolism, the green plant produces far more oxygen than it utilizes. In this respect, green plants serve the oxygen requirements of animals and heterotrophic plants, which in turn produce the carbon dioxide that is vital to the life of the green plant. Hence, the world of life is involved in a gaseous cycle in which oxygen and carbon dioxide play the predominant roles. In nutrient interrelations, plants and animals also balance each other.

Returning to our hypothetical green plant, let us suppose that it is a perennial plant (perhaps an oak tree) which has reached an age of fifty years. How much respiration occurs in such a plant, and in what areas? Actually, a great portion of such a plant is composed of dead tissues, including almost all of the cells of the main body from the bark inward, as well as much of the bark. The same is generally true of the root system. In the main, living cells are restricted to the growing tips of stems and roots, a thin layer of the bark, and the current crop of leaves during a growing season. This knowledge can sometimes be put to practical use. For example, a tree may be killed by the addition of soil around its trunk, and this should be avoided as a horticultural practice. This apparently interrupts the flow of oxygen to root tissues which remain active in respiration. Again, pruning a tree very closely may kill it, especially during the growing season, as the living cells have been decreased below a critical point.

6.3 Metabolism is the total chemical activity of a given living system. **Summary** Regardless of the level at which it is considered, three phases are apparent: nutrition, synthesis, and respiration. From a thermodynamic viewpoint, a given metabolic reaction is either catabolic

(exergonic) or anabolic (endergonic) Both nutrition and respiration involve a preponderance of catabolic reactions, whereas synthesis is essentially anabolic.

At the cellular level, we can distinguish cells nutritionally according to whether they synthesize organic compounds from inorganic precursors or whether they are dependent upon prefabricated organic molecules. In any event, organic molecules (chiefly carbohydrates and lipids) ultimately furnish most of the free energy of the cell. These organic molecules contain chemical energy which originally existed as radiant energy, and which was "captured" during photosynthesis. This is an extremely complex process involving a light phase, during which radiant energy is transferred to certain electrons of chlorophyll, and a dark phase, during which carbon dioxide is "fixed" in the form of carbohydrates. Other synthetic processes within cells account for the build-up of a great variety of organic compounds. In respiration, organic molecules are degraded, with the result that low-energy chemical bonds are "concentrated" into high-energy phosphate bonds of ATP molecules. Respiration consists of anaerobic and aerobic phases. The anaerobic phase results in relatively little energy transfer, whereas the aerobic phase includes the major energy transformations from low-energy to high-energy bonds. During the aerobic phase, the end product of anaerobic respiration, pyruvic acid, is oxidized to carbon dioxide and water. The actual chemical breakdown occurs in the Krebs cycle, and energy transferral to ATP occurs primarily in the cytochrome oxidase system.

At the organismic level, metabolism includes those chemical activities which are cellular, and in addition, certain reactions which do not occur within cells. In the complex animal body, such as that of the human, nutrition is achieved by means of materials which are brought into the body from an external source, and digestion of fuel nutrients occurs in the gastro-intestinal tract. Synthetic activity involves the utilization of organic molecules resulting from digestion, as well as inorganic substances which are brought into the body. Such synthetic activities account for the production of new cellular materials, as well as the production of waste substances which are eliminated from the body. Respiration in the complex animal body occurs at the cellular level, and in addition, this term is made to include those activities by means of which the organism exchanges gases with its environment. All three phases of metabolism (nutrition, synthesis, respiration) are interconnected in a highly complex fashion, and involve many organ systems, for example, the blood-vascular system. Balance among these phases is such that the organism displays an overall homeostasis. While metabolism in a green plant is

markedly different from that in a complex animal, it is also represented by the phases of nutrition, synthesis, and respiration. The green plant absorbs water and minerals through its root system, and gaseous exchange with its environment occurs principally through its leaves. Photosynthetic activity accounts for the buildup of carbohydrates in the plant, and these may be utilized in the synthesis of other types of organic molecules. Respiration occurs in plant cells in similar fashion to that in animal cells, although in contrast to the more complex animals, there are no elaborate breathing and transport mechanisms associated with plant respiration.

Questions

1 Early in this chapter, we contrasted a living system with a gasoline engine, and we said that the fundamental difference lies in the inability of the engine to repair itself through self-perpetuation of vital parts. Suppose a machine, perhaps a supercomputer, were invented which possessed the capacity for self-perpetuation, including the ability to reproduce itself. Would it be "alive"? Defend your answer.

2 As you learned in this chapter, several factors govern the passage of molecules or ions through cell membranes. In the case of each substance listed below, which of these factors might best explain its penetration of the membrane as indicated? (a) The entrance of Cl^- into the cell, (b) the entrance of water into a flaccid cell; (c) the absorption of chylomicrons into the lymphatic capillaries from the small intestine, (d) the entrance of glucose into the cells lining the cavity of the small intestine against a concentration gradient; (e) the secretion of large enzyme molecules from the cell to its environment.

3 Distinguish among photosynthesis, chemosynthesis, and organosynthesis. Do all cells exhibit each type of synthesis? Explain.

4 What is the relationship of oxidation and reduction to energy changes? Give a specific example from a living system.

5 Contrast the light and dark phases of photosynthesis with regard to their respective roles in the transformation of radiant energy to chemical energy.

6 Contrast anaerobic and aerobic respiration with respect to their relative efficiencies in ATP production.

7 What is the chief function of the Krebs cycle? Of the cytochrome oxidase system?

8 What is the functional role of mitochondria in the cell? Incidentally, mitochondria have not been demonstrated in bacteria, and yet most species of bacteria carry on the activities which are usually associated with mitochondria. Apparently, the cell membrane as-

sumes these functions in bacteria. What physical characteristics might we assume of bacterial cell membranes that we would not assume of the membranes of cells which contain mitochondria?

9 Trace the pathway of a bite of food containing all three food types from the time that it enters the mouth of a human to the time that its components are absorbed into the intestinal wall. Now assume that one glucose molecule enters a cell and is subjected to complete respiration. Tell what happens in this process.

10 The term respiration is defined somewhat differently at cellular and organismic levels of organization. What is this difference?

11 In answering the test question "How do plants and animals differ with regard to their utilization of gases?" a certain student wrote that "animals breathe oxygen, but plants breathe carbon dioxide." Had you been the teacher, what explanation would you have given the student if he protested that he had answered the question correctly?

12 It might seem rather odd to you that we included a discussion of waste elimination from the human body under the topic of synthesis. In what way or ways is synthesis involved in waste elimination?

13 What are the functions of the liver in the complex animal body?

14 Some plant physiologists maintain that water pressures developed in roots account for a major part of the upward movement of water in a complex plant body. Could you devise an experiment that might indicate the relative importance of root pressure and transpiration with respect to this process? Galston (see reference below) discusses this problem; you might be interested in reading his presentation.

15 Hydroponic gardening involves growing plants in water rather than in soil. With many plants, such as tomatoes, a much greater yield can be obtained per unit of water area as contrasted with a similar area of soil. What advantages might hydroponic gardening have over soil gardening? What special problems might one encounter in hydroponic gardening?

References

Galston, A. W. *The Life of the Green Plant* (2nd ed.) Englewood Cliffs, N.J.: Prentice-Hall, Inc., 1964. One of the Foundations of Modern Biology series, this book will be especially helpful with regard to photosynthesis and other aspects of plant metabolism discussed in this chapter.

Langley, L. L., and E. Cheraskin. *Physiology of Man* (see reference at end of Chapter 5). An excellent presentation of human biology that will serve as good collateral reading for parts of this chapter.

McElroy, W. D. *Cellular Physiology and Biochemistry* (see reference at end of Chapter 5). This book is recommended in its entirety to be read in connection with this chapter.

Schmidt-Nielsen, K. *Animal Physiology* (2nd ed.) Englewood Cliffs, N.J.: Prentice-Hall, Inc., 1964. This book is another in the Foundations of Modern Biology series; much of it is devoted to topics that are covered in this chapter.

In addition to the books above, the following articles from *Scientific American* are recommended. Those marked with an asterisk are included in *The Living Cell* (see reference at end of Chapter 3), which features several other articles related to metabolism.

*Arnon, D. I. "The Role of Light in Photosynthesis," Vol. 203, November, 1960. Some of the mechanisms involved in the transformation of light energy into the potential energy of carbohydrates are discussed in this article.

Fenn, W. O. "The Mechanism of Breathing," Vol. 202, January, 1960. The structure and function of the human lungs and their accessory structures are discussed.

*Green, D. E. "The Mitochondrion," Vol. 210, January, 1964. A discussion of the role of mitochondria in respiration.

*Lehninger, A. L. "How Cells Transform Energy," Vol. 205, September, 1961. An excellent discussion of energetics with particular emphasis upon photosynthesis and respiration.

Smith, H. W. "The Kidney," Vol. 188, January, 1953. An account of the structure and function of the human kidney.

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Growth

7

Having discussed the phenomenon of metabolism and the activities which accompany it, we are now in a position to comprehend a second characteristic of living matter, growth, which is made possible in an organism by virtue of anabolic processes resulting in the synthesis of protoplasm. The ability to utilize materials found in its environment for the production of more complex substances gives protoplasm a unique distinction; although crystals or rocks may "grow" by the accumulation of various materials, this is hardly comparable to the complex metabolic activities exhibited by protoplasm in adding to its own total quantity. It becomes our present task to direct attention to different circumstances under which growth may occur, various types of growth, and the specialization of cells and tissues which occurs in the phenomenon called *differentiation*.

- The biological meaning of growth**
- 7.1 By definition, growth simply means *increase in mass*. This increase in mass is due to the synthesis of cellular protoplasm or intercellular material formed by the cells, exclusive of waste materials or secretion products. Although the imbibition of large amounts of water and the intake of food materials certainly bring about an increase in mass, such an increase before digestion, absorption, and metabolism have taken place should not be considered growth. From a metabolic standpoint, growth constitutes a preponderance of anabolic (synthetic) processes in an organism over those which are catabolic (decompositional).

When the biologist states that growth is a characteristic of living systems, he does not mean that every organism is adding to its total quantity at all times or that every cell in a complex body is synthesizing more protoplasm. Although most plants continue to grow as long as they live, it is characteristic of most animals to reach a certain size at which point further overall growth is not necessarily demonstrated. At this point, catabolic and anabolic processes are in quantitative equilibrium. The statement that growth is a characteristic of living systems means that protoplasm exhibits the *potentiality* of growth, although in cases where cells are sufficiently specialized as to have lost the ability to increase their total mass, this potentiality may be limited to the replacement of degenerating cellular parts.

- The major levels of growth**
- 7.2 Growth may occur at different levels in a living system. In order to see that growth is a universal characteristic of living systems, let us consider its occurrence at various levels of organization.

Cellular and intracellular levels of growth At the cellular and intracellular level, growth involves cell division and intracellular synthesis. The cell divides into two cells, and by subsequent intracellular synthesis, the two cells attain the size of the original cell. The

process may be repeated in each of these two cells, then in their progeny, with the result that an overall exponential growth results. The forces which initiate the process of cell division are not quite clear, but division of a given cell is usually preceded by the synthesis of sufficient protoplasm that, when the cell reaches its maximum size, division occurs to produce two daughter cells from the original one. Cells exhibiting a high degree of metabolic activity, for example bacterial cells under optimal conditions, may divide as frequently as every fifteen or twenty minutes. There is remarkable uniformity among organisms with regard to the mechanics of cell division. With the exception of certain forms, division may be said to consist of two processes, namely, nuclear division, or *mitosis*, and cytoplasmic division, or *cytokinesis*.

Division of the nucleus—mitosis The first indication that a cell is about to undergo division is a visible change in the chromatin "network" of the nucleus. Special staining and microscopic techniques reveal that this material is not really a network at all but that it consists of elongated threads which are distinct from each other. As the nucleus undergoes further change, these threads gradually condense and thicken. Because this is the first and most obvious of the nuclear changes associated with division of the nucleus, early cytologists settled upon the name mitosis (Gr. *mitos*, a thread) to describe the entire process of nuclear division. From the beginning of the mitotic process to the formation of two daughter nuclei, four progressive and interconnected stages or phases are recognized.

PROPHASE This stage begins with the condensation of the chromatin threads, which are called *chromosomes* as they become distinctly visible (Figure 7.1). The number of chromosomes which finally make their appearance at late prophase is generally constant for a species; for example, the cells of the onion (*Allium cepa*) exhibit sixteen chromosomes, and those of the parasitic roundworm *Ascaris lumbricoides* possess only four. These two species are mentioned as examples because they are frequently used to demonstrate mitosis to beginning students. The chromosome number per human cell is forty-six. In the cells of some organisms, the chromosomes number into the hundreds. Apparently, there is no correlation between chromosome number and degree of complexity of an organism.

Great variation in chromosomal morphology occurs among species, there being differences both in size and shape. Even within a species, the chromosomes can often be distinguished from one another, and can be named or numbered on that basis. In the cells of the great majority of organisms, a given chromosome is seen to have a morphological partner, that is, the chromosomes exist in pairs, although paired chromosomes show no tendency to associate closely

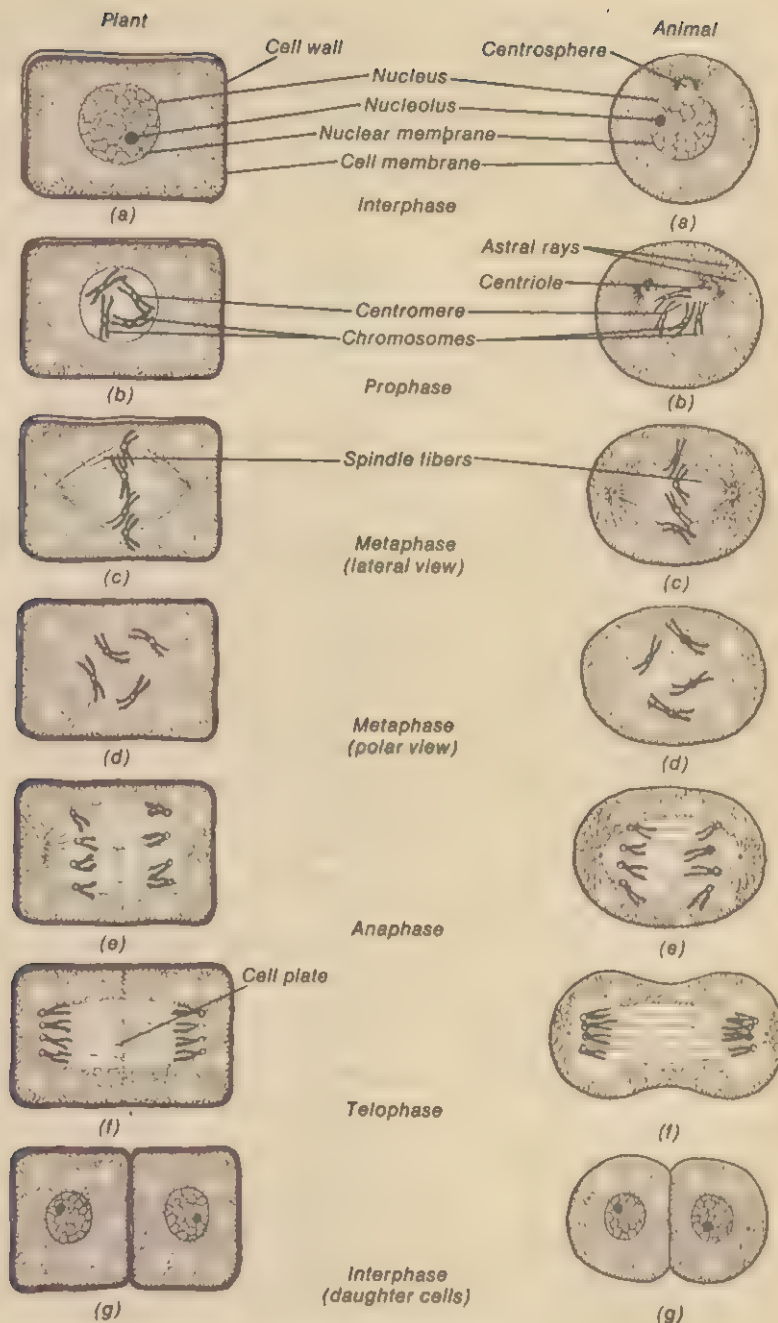


Figure 7.1 A comparison of plant and animal cell division. Each type of cell is shown as having four chromosomes.

in the nucleus.* Hence, it is frequently said that an organism exhibits a certain number of chromosome pairs; onion has eight pairs, *Ascaris* has two pairs, and so on. As will be emphasized in a later chapter, the members of these pairs are the descendants of those contributed by the individual's two parents.

If the chromosomes are closely examined as they become visible at prophase, they will be seen to consist of two parallel halves called *chromatids*, which are connected by a *centromere* (Figure 7.1). Hence, this stage of mitosis reveals the presence of twice as many chromatids as there are chromosomes.

At some time during prophase, the nucleoli and nuclear membrane disappear. The full significance of this is not completely understood, but one immediate result is that the nucleoplasm is no longer separated from the cytoplasm. Consequently, beginning with late prophase, a cell does not really possess a nucleus during its division, even though we speak of "nuclear division."

METAPHASE Near the end of prophase, the chromosomes become oriented in such a way that a lateral view of the cell shows that the chromatids of a given chromosome are in position to move toward opposite poles of the cell; at the point when the centromeres of all the chromosomes are so oriented as to lie in an equatorial plane (Figure 7.1c), metaphase is said to begin. In a polar view of the cell (Figure 7.1d), a ring or plate of chromosomes is characteristically seen, and this is usually the most advantageous view for counting or studying the chromosomes. Meanwhile, a *spindle*, so called because of its shape, appears in conjunction with the orientation of chromosomes, and some of the *fibers* which compose it attach to the centromeres of the chromosomes, while others simply run from pole to pole.

Perhaps the most significant event which occurs during metaphase is the division of chromosomal centromeres. This results in the possession of a centromere by each chromatid. Half the original number of chromatids (now called *daughter chromosomes*) are thus prepared for movement toward one pole and half toward the other, each set constituting the chromosomal complement of a daughter nucleus.

ANAPHASE With the division of centromeres, which occurs simultaneously in all the chromosomes of a given nucleus in most cases, *anaphase* begins. There is a shortening of those spindle fibers that attach to the centromeres of daughter chromosomes, as though a pulling force were being exerted. Actually, the forces responsible for

* Paired chromosomes do become closely associated during a special type of nuclear division called meiosis, which we will discuss in a later chapter.

chromosomal movement in this situation are not clearly understood, but the attachment of spindle fibers to the centromeres is suggestive of some active role by the fibers in chromosomal migration. At late anaphase, chromosomes which are moving toward opposite poles of the cell are widely separated (Figure 7.1e).

TELOPHASE Telophase begins when chromosomal migration is complete, and it is somewhat the reverse of prophase. The chromosomes gradually lose their apparent individual identity and they collectively form the chromatin "network," or mass, typical of a nucleus that is not involved in division. Nucleoli and the nuclear membrane reappear, and telophase ends when the two daughter nuclei are identical to the original nondividing nucleus except in size.

A nucleus which is not undergoing mitosis is said to be in *interphase*. In actively dividing cells, this is a period of synthesis and growth on the part of the nucleus, which enables it to enter again into mitosis at a later time. During interphase the chromosomes lose their definite stainability, but it has been shown that their individual identity is retained. In other words, chromosomes are not dissolved and reformed at telophase and prophase respectively; they simply assume different morphological forms.

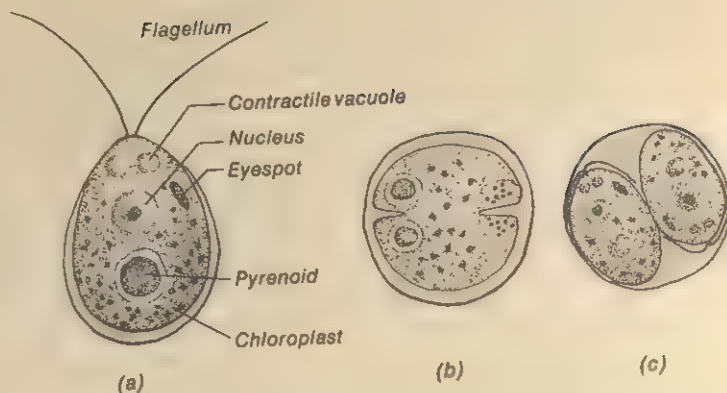
It should be recognized that the stages of mitosis are portions of a continuous division cycle and that there is no definite point between each; the phases are recognized by cytologists simply as convenient divisions for reference purposes. By observing the process closely with proper optical equipment, it can be seen that the nucleus moves smoothly from one phase to another.

Intimately associated with the process of mitosis in animal cells is the behavior of the centrosome and centrioles. During prophase the centrosome divides and each half undergoes migration in such a way that the two centrioles lie opposite to each other. At metaphase, a centriole is thus situated at either side of the nucleus, and each serves as a center from which the spindle fibers and *astral rays* radiate (Figure 7.1c). Plant cells, except for those of certain lower forms, do not exhibit centrioles. Nevertheless, a spindle is generally formed, although *astral rays* are not.

Division of the cytoplasm—cytokinesis The process of cytokinesis, consisting in a given cell of some mechanism whereby the cytoplasm is separated into two more or less equal parts, is considerably less dramatic than that of mitosis. Usually, cytoplasmic organelles or inclusions such as mitochondria or plastids are distributed more or less equally in the process.

In animal cells, cytokinesis is accomplished by *constriction*, the process generally being initiated at about the time of mitotic anaphase. By the end of telophase, when daughter nuclei are fully

Figure 7.2 *Chlamydomonas eugametos*. (a) Individual organism; (b) telophase of mitotic division within cell wall, cytokinesis almost complete; (c) two daughter cells within old cell wall



formed, constriction is complete (Figure 7.1g). A variation of constriction is seen in the furrowing process characteristic of certain embryos and other cellular aggregates in which groups of cells divide simultaneously and remain in close contact with each other following cytokinesis.

As an accompaniment of their cellulose walls, whose rigidity renders constriction impossible, plant cells exhibit a mode of cytoplasmic division different from that described above for animal cells. Cytokinesis begins in the plant cell by the formation of a *cell plate* in the middle of the cell at about the time mitotic anaphase ends (Figure 7.1f). The cell plate continues to grow in circumference until it meets the outer walls of the cell. In the meantime, the nucleus has progressed from telophase to interphase, and division of the cell is completed by differentiation of a new cell wall on both surfaces of the cell plate.

In certain plants, cytokinesis is somewhat animal-like. For example, dividing cells of the green alga *Chlamydomonas*, which is unicellular, undergo constriction of the protoplast within the cell wall. Each division product may undergo subsequent divisions, but at any rate, daughter cells will have secreted new cell walls when the original wall breaks open and releases them (Figure 7.2).

Except for certain minor variations, cell division is a remarkably uniform phenomenon among organisms. This is highly significant, since it lends further support to the view that living forms are fundamentally similar. Whatever the physical and chemical factors involved, mitosis is an effective means for ensuring a qualitatively and quantitatively equal distribution of certain key nuclear substances to newly synthesized cytoplasm. As we have already observed, the chromosomes are bearers of hereditary determiners (genes), and it is significant that each cell of an organism normally possesses exactly

the same complement of these as any other cell. The process of mitosis makes this possible. Because it can produce more cells, a given multicellular organism is able to increase its own body mass, undergo histological specialization, and repair tissues through cell replacement. As a fundamental biological process, therefore, cell division ranks exceedingly high.

Cell division and synthesis Since the chromosomes are duplicated and separated in the process of cell division, it is obvious that the major macromolecules (DNA, protein) which constitute chromatin must be synthesized at some time in the life cycle of a cell. In addition, the original cell size cannot be attained without the synthesis of RNA and cytoplasmic protein, to say nothing of less complex molecules. Even in the most actively dividing cells, there is a period (interphase) when the cells are not undergoing actual division. It is during interphase that a great deal of the synthesis (thus increase in mass) takes place. As a result, cells which emerge from an active division attain the typical cell size (for that particular cell type), and they also possess the amount of DNA necessary for chromosomal duplication during the next divisional cycle. Figure 7.3 represents the cyclic nature of events in cells which are mitotically active.

Since we discussed the descriptive phases of mitosis earlier, let us now attempt to understand something of the intracellular synthesis which occurs during the cycle. The time relationships involved (Figure 7.3) are highly variable in different organisms and in different

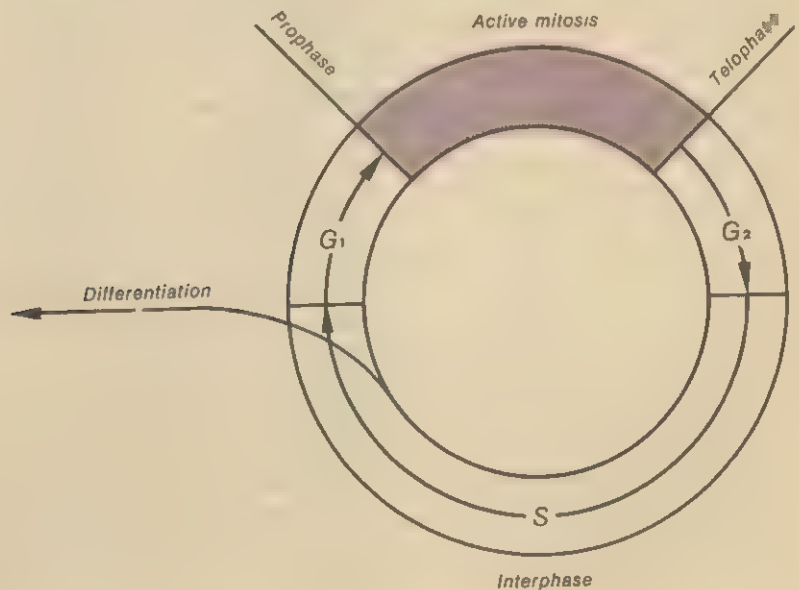


Figure 7.3 Graphic illustration of the synthetic-divisional cycle exhibited by cells in active division. During the gap periods (G_1 and G_2) no DNA is synthesized. Total DNA is doubled during the synthetic (S) period. Instead of continuing in active division, a cell may follow the pathway of differentiation. ■

cell types of the same organism. Furthermore, variations in the environmental circumstances (for example, temperature) under which cells are growing have an important bearing upon length of the cycle. However, we can make some fairly accurate generalizations with regard to the different periods of the cycle, and as we shall see, these generalizations are related to the synthetic activity which is taking place.

Experiments involving radioactively labeled precursors of DNA, RNA, and protein have provided a rather clear picture of the points in the cycle at which these macromolecules that are so important in the control of cellular metabolism are synthesized. These experiments indicate strongly that the synthesis of DNA is restricted to the S (synthetic) period; there is no incorporation of labeled DNA precursors during active mitosis when the chromosomes are undergoing contraction and division, nor during the G_1 (gap 1) and G_2 (gap 2) periods immediately preceding and following active mitosis. The total quantity of DNA is doubled during the S period, which provides a full complement of DNA for the prospective cells that will result from the next active division.

The synthesis of RNA occurs between late telophase and early prophase. Thus, RNA synthesis is completely stopped only when the chromosomes are in a contracted state. However, during the S period when DNA is being synthesized, the synthesis of RNA is greatly reduced. This indicates that during the S period all of the DNA is not being replicated at the same time; some RNA may be templated.

Protein synthesis occurs throughout the entire cycle, although it occurs at a reduced rate during the stages of active mitosis when the chromosomes are in a state of maximum contraction. In the light of what we know about the control of protein synthesis, this indicates that enough messenger RNA is synthesized in early prophase to permit protein synthesis to continue through the other stages until late telophase, at which point more messenger RNA is templated by DNA.

In summary, intracellular growth occurs whenever synthetic processes result in a greater amount of protoplasm within a given cell. This ordinarily leads to cell division, and with further synthesis and subsequent division, the overall growth of a group of cells occurs. In most cases, then, growth (increase in mass) is the result of an increase in cell number.

The organismic level of growth Growth at the organismic level is a reflection of growth at the cellular and intracellular levels, since the fundamental unit of mass or structure is the cell. Therefore, at the organismic level, growth may be the result of an increase in cell number, an increase in cell size, or a combination of the two. Of these possibilities, overall growth is rarely the result of an increase in

cell size exclusively, although this is known to occur. In certain nematodes, for example, the number of cells in the adult is approximately the same as that of newly-hatched individuals. In most organisms, growth is the result of a combination of both increase in cell size and in cell number. In embryonic stages prior to cell specialization or differentiation, the cells increase in number by division. However, as certain cells begin to specialize they fail to cycle back into active mitosis; instead, they proceed along a certain path of differentiation (Figure 7.3). This specialization is accompanied by intracellular synthesis, which results in an increase in cell size. Nevertheless, certain cells retain the capacity for active division and account for a major part of the growth that occurs from the immature stage to the adult stage.

As we mentioned previously, most animals reach a point at which overall growth ceases. At this time, those cells which are actively dividing merely replace cells that are degenerating. For example, human red blood cells are destroyed and replaced continuously, as are cells in the outer layer of the skin. In contrast, muscle cells may increase in size throughout most of the life of the individual, depending upon diet and exercise. In higher plants, certain cells retain the capacity for active division throughout the life of the organism, and instead of replacing cells which degenerate (as is the case in the more active animal body), they merely add to the total mass. As a result, growth continues throughout the life of the plant.

Although growth may assume different forms in various organisms, or in different tissues of the same organism, it is a universal characteristic of protoplasmic systems. The intricate mechanisms controlling growth in organisms are incompletely understood at the present time, but eventually, many of them will undoubtedly be elucidated. When this occurs, it is reasonable to predict that such factors will be discovered at the cellular level. Because of this, research in the areas of cell division and intracellular synthesis continues to be very active.

7.3 It should be obvious by this time that protoplasm is an extremely versatile material. Although it exhibits basic characteristics which are found universally, variations exist in its chemical and physical constitution. Were this not the case, all cells, tissues, and organisms would be exactly alike.

The phenomenon of differentiation Cells and protoplasmic structures may become so organized as to perform specialized tasks that other cells or structures do not perform. The process by means of which such specialization is achieved is termed *differentiation*. The differentiation of cells is most clearly

demonstrated by the changes which occur in embryonic tissues of plants and animals between the time they arise by division of a parent cell and the time when they become fully specialized. The causal mechanisms leading to differentiation are not entirely clear, although some insight has been gained.

As one studies the development of complex organisms from the one-celled stage to the highly organized adult form consisting of possibly trillions of cells, each with its particular functional specialization, the entire spectrum of organizational levels is encountered. Specialized cells appear which are associated together in the formation of specific organs, and finally, organ systems are coordinated in the organism.

The term differentiation may be used in a very broad sense to cover this entire spectrum of activity, or it may be used in a number of more restricted senses. Many biologists refer to the specialization of cells from a condition of apparent morphological and functional uniformity to a specialized state as *histological* differentiation. This process involves the chemical and structural changes which take place at the intracellular, cellular, and tissue levels. Simultaneously with histological specialization, certain regions of the embryo undergo differentiation, that is, gross tissue organization occurs. For example, in the development of higher animals, one can identify a brain region as compared with other regions, and later, a forebrain, a midbrain, and a hindbrain are all discernible. Many biologists refer to such changes as regional differentiation or simply *regionalization*. At the same time, various organs assume their particular forms, and finally, the entire embryo takes on a specific morphological appearance. Differentiation at this higher level of organization is called *morphogenesis*. The noted embryologist C. H. Waddington has referred to these three aspects of differentiation as differentiation in time (histological differentiation), differentiation in space (regionalization), and differentiation in shape (morphogenesis).

The sense in which we introduced the concept of differentiation at the beginning of this section—the sense in which the term is used most often—relates more directly to histological differentiation (differentiation in time) than to regionalization or morphogenesis. It is primarily to this aspect of differentiation that the following remarks are related.

Perhaps an analogy will serve to clarify these processes, at least with regard to their significance. In our society, we produce children who are destined to become specialized members of a complex social group. To a certain age, they are much alike except in potentiality and environment. They all attend school and study the same subjects, and at least until they finish their early education, they are

not much different from each other as far as society and their roles in its behalf are concerned. They are merely students. Gradually, however, they are led into different fields of endeavor. By the time a given class of unspecialized twelve-year-olds has reached the age of thirty, great diversification has taken place. One person is a physician, another a teacher, still another an electrician, and so on.

In a metaphorical sense, such individuals are the "cells" of a societal organism, and their specialization parallels in certain ways that of cells which develop in an actual organism. Furthermore, as is the case with their societal analogues, the factors which contribute to the ultimate fate of a given cell or its progeny are quite complex. It is entirely beyond the scope of this book to attempt a detailed account of the mechanics of differentiation in various organisms, but perhaps mention of experimental approaches to the problem and some of the factors that have been discovered will be enlightening. The problem may be defined by referring back to Figure 7.3., which shows a mitotic cycle. What are the factors which start a given cell toward differentiation instead of cycling back into active mitosis? Put in other terms, what shuts off mitosis and turns on differentiation? We cannot answer these questions fully, but perhaps we can suggest some interesting possibilities.

Generally speaking, there are two classes of factors which determine the fate of a given cell and its division products. Certain of these factors are *intrinsic*—localized within the cells themselves—while others are *extrinsic*—they depend upon influences which are external to the cells. Let us consider these two classes of influencing factors in turn.

As a cell or a group of cells becomes specialized in structure and function, regardless of the final differentiated state, there must be accompanying chemical changes. In the main, these changes involve the elaboration of different structural and functional (enzymatic) proteins. It should be apparent by this time that what a cell can do is a reflection of the particular protein composition of the cell, that is, the type and arrangement of structural and enzymatic proteins that control the metabolism of the cell. In view of this, the embryologist S. Spiegelman has called differentiation "the controlled production of different enzyme patterns."

At this point, it may be helpful to review Section 5.2, where we discussed the control of protein synthesis. In the light of these concepts, it would be tempting to view the DNA units (genes) as the sole and complete factors which initiate and control development. Thus, the development of an organism would simply be the progressive unfolding and expression of the encoded information of the DNA complement as it directs the enzymatic patterns which lead to

the final differentiated state. However, this is not the case. Since the multicellularity of the embryo results from repeated cell divisions, in which process the chromosomes containing the genes are simply equated in the new cells, it is reasonable to assume that all cells of the organism possess identical genetic complements. The question then arises as to why every cell of the organism does not exhibit identical patterns of differentiation. Since they obviously do not, it seems reasonable if not essential to assume that there must be other intrinsic or extrinsic factors which play a part in the initiation and control of differentiation.

The eggs of many species of animals show very distinct cytoplasmic regions. These visibly different regions are the result of a differential concentration of yolk, pigment, and other materials. Even in eggs which show no visible regional differentiation in the cytoplasm, metabolic gradients exist as a result of chemical differences in contrasting areas of the egg. Sea urchin eggs, discussed below, exhibit such metabolic gradients. There is a considerable amount of experimental evidence which indicates that as the fertilized egg divides and a multicellular complex is formed, the daughter nuclei (containing identical DNA) may become located in diverse cytoplasmic environments. Therefore, certain cytoplasmic factors may initiate the process of cell differentiation by acting upon the genetic material in different ways. For example, a substance present in the cytoplasm of one daughter cell but not in that of another might act as a derepressor (see Section 5.2), thus interfering with the influence of a repressor gene upon a substrate. Thus, a differential genetic activity is initiated in cells of different regions. Perhaps we can visualize how "derepressed" genes control the release of messenger RNA into the cytoplasm, where protein synthesis takes place. The introduction of new protein molecules changes the molecular ecology of the particular cell, and if these proteins are absent in some contrasting cell, then it is not difficult to see that subsequent events in differentiation will probably not be the same in the two cells. Thus, a given cell may develop a complicated feedback system which leads to a particular channel of differentiation.

As an example of experiments which show that normal development and differentiation of embryonic cells are dependent upon intrinsic factors, let us consider the work of certain investigators on embryos of the sea urchin. The egg of the sea urchin exhibits a distinct polarity; we refer to the more metabolically active end of the egg as the *animal pole*, whereas the opposite end is called the *vegetal pole*. A straight line connecting the two poles would constitute an *animal-vegetal axis*. A definite metabolic gradient exists along the animal-vegetal axis, which implies a difference in the chemical

constitution of the cytoplasm in the two contrasting regions. Normally, the first division plane of the sea urchin egg parallels the plane of the animal-vegetal axis. If the two resulting cells are shaken apart under appropriate conditions, each will develop into a normal sea urchin larva. Since the division plane is parallel to the animal-vegetal axis, the two cells will contain approximately equal amounts of cytoplasmic materials present in both animal and vegetal portions of the egg. The second division plane is also parallel to the animal-vegetal axis, but at right angles to the first division plane. This division produces four cells from two, each containing approximately equal amounts of the same kind of cytoplasmic material. When these four cells are shaken apart and permitted to undergo further development, each develops into a normal sea urchin larva. The third divisional plane is perpendicular to the animal-vegetal axis, and as a result of this division, two tiers of four cells each are formed. Thus, the four cells of one tier are derived from animal pole cytoplasm while those of the other tier are derived from vegetal pole cytoplasm. When these cells are isolated, they do not develop into normal larvae (Figure 7.4).

In addition, it is possible to divide the sea urchin egg into animal and vegetal halves and fertilize each half, or to cause the first divisional plane of a fertilized egg to be shifted so as to divide the egg into an animal half and a vegetal half. In neither case does normal development occur when the two halves are separated (Figure 7.4). It appears that a differential distribution of cytoplasmic factors along the animal-vegetal gradient precludes development. However, some animal embryos divide in such a way that a differential distribution is initiated at the first cleavage.

Experimental studies indicate that extrinsic factors (those which are external to a cell and which influence its development) also play an important role in development. For example, the differences in oxygen availability and the opportunity for waste removal which exist between cells at the surface of an embryo and those that lie more deeply result in different metabolic and divisional rates. Furthermore, chemical influences from one cell group to another are known to prevail. In a vertebrate embryo, groups of cells develop as "organizers," and this is the first stage in differentiation of cells to form specific organs. These organizers influence cells around them, which are as yet undifferentiated, to form certain tissues. That this influence is a chemical one is shown by the phenomenon that induction may be effected by the use of extracts from organizer cells. For instance, the first organizer to form in the frog embryo is a certain patch of tissue which influences, among other things, the development of the nervous system. If cells of this organizer are

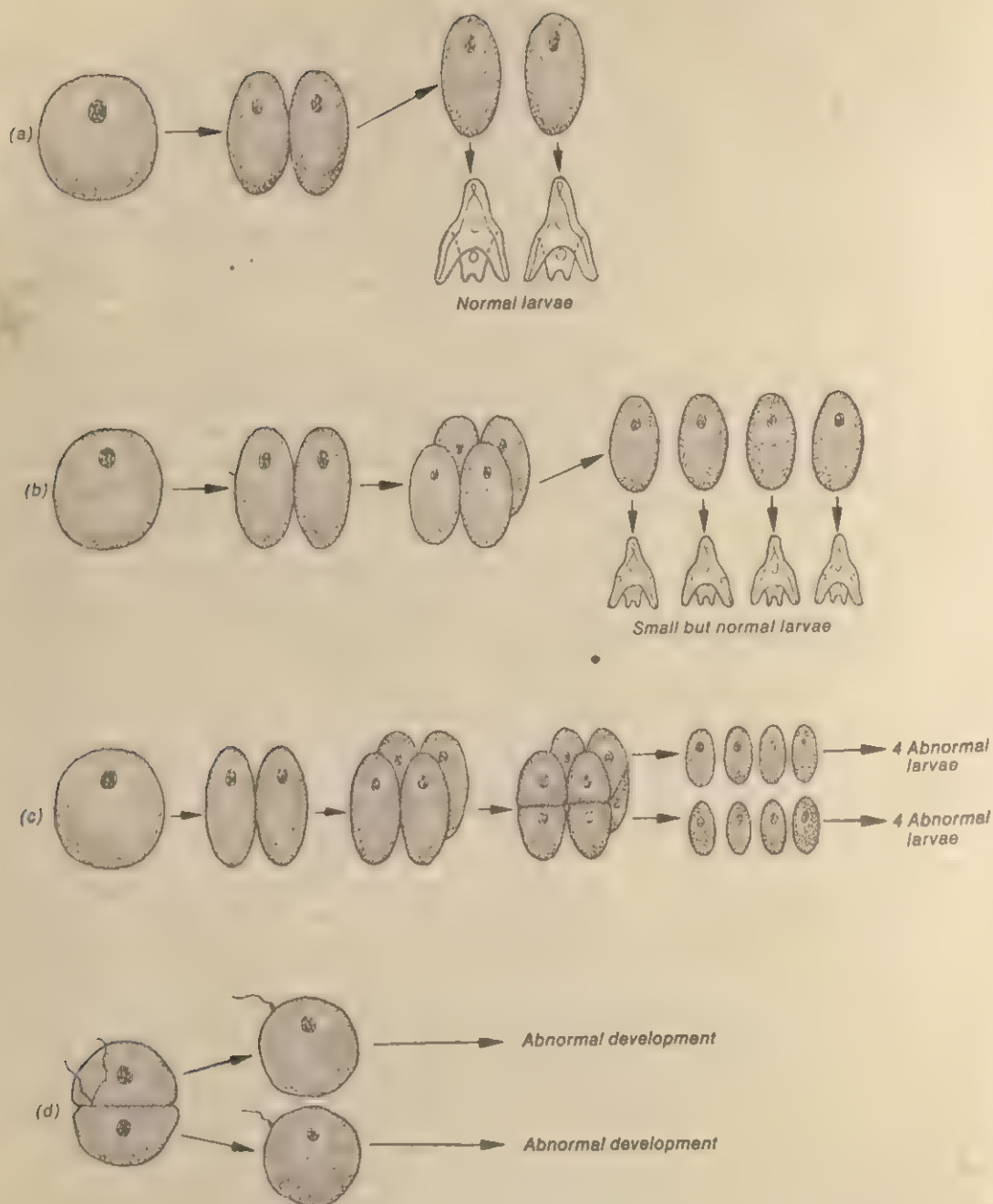


Figure 7.4 Diagram of experiments on sea urchin development. See text for amplification.

transplanted to a portion of the embryo far removed from the normal site of nervous system development, they induce a nervous system there. However, it is not necessary to transplant the cells themselves; if they are destroyed and extracts of their contents are injected just beneath the surface of an embryo at some point of its body, a nervous system will develop at that point. In other words, such experiments as this indicate that substances from one cell group may pass into another cell group in the normal embryo with the result that the latter cells are influenced to differentiate along certain lines. Thus, any such chemical substances constitute extrinsic factors as far as the influenced cells are concerned, even though they are not extrinsic to the embryo itself. Much is yet to be learned about the exact chemical basis for such influence, but organization and induction are very important factors in differentiation.

Aside from the fundamental causes, or the *how* of cell differentiation, embryologists have gained much information about the actual processes, or the *what*, in several types of organisms. In animal embryos, for example, cells or groups of cells may be marked in various ways and can thus be traced. It has been common to use harmless dyes, graphite, or other such materials for marking cells. Similarly, methods for studying cellular differentiation have been developed with regard to plants. From such studies, a wealth of information has been gained regarding the ultimate fate of various embryonic plant and animal parts.

Thus far in our consideration of differentiation, we have thought largely in terms of *histological specialization*, that is, the development of cells to form a part of some tissue which is known by its particular function. How can we account for the ability of unicellular organisms to exhibit within a single cell the many accomplishments necessary to the maintenance of life? It must be concluded that a cell such as *Amoeba* is obliged to be a jack-of-all-trades in its activities, and any differentiation within its protoplasm is of necessity based on *cytological* specialization of cell organelles. A great deal of research has been directed toward the identification of structure with function in such organisms, and much evidence for a high degree of specialization has accumulated. For example, as we have seen, removal of the nucleus from *Amoeba* by microdissection results in a cell which may live and carry on some activities for a time, but loss of the nucleus is accompanied by a loss of such vital activities as protein synthesis. These activities may be restored if a nucleus from another amoeba is transplanted into the cell. It has been shown by centrifuging mitochondria from cells and testing them for physiological properties that they serve as storehouses for enzymes without which the cell could not carry on respiration. Other organelles of the

cell have been similarly shown to perform definite and specific functions.

Actually, all cells exhibit a high degree of cytological differentiation, as is shown by the well-nigh universal appearance of nuclei, mitochondria, and certain other organelles. The organization of an endoplasmic reticulum, which was previously noted, indicates a high degree of structural organization. It will be recalled that the sea urchin egg is organized in such a way as to require early divisions in a certain plane for normal development to occur. Thus, it should not be thought that cells of multicellular organisms are specialized past all cytological differentiation; some, in fact, are hardly specialized at all histologically. The unicellular forms are the Robinson Crusoes of the cell world, and cells such as nerve cells of higher animal bodies are the physicians, teachers, and electricians of a complex society. The physician is, nevertheless, obliged to retain certain unspecialized abilities to at least a degree; he can still drive a nail or change an automobile tire, although he is neither a carpenter nor a mechanic. In the same way, even highly specialized cells retain some of their unspecialized abilities. For example, liver cells of higher animals are more active in metabolism than most cells, but all carry on metabolism to some degree. Nerve cells are specialized in the conduction of impulses, but all cells are somewhat capable of this.

One of the many outstanding biological principles which have come to be recognized as a result of such cell studies as those described above is that unicellular organisms are no less complex than their multicellular superiors except in a purely organizational sense. It is simply that their organization is completely *cytological* rather than being partially *histological*. This has resulted in a revised viewpoint toward the so-called simple organisms and has bred a profound respect for protoplasm and its complexities in all life.

7.4 Growth and differentiation in animals

Early embryogeny of multicellular animals Although some of the lower multicellular animals reproduce by the development of new individuals from single, uniparental cells or aggregates of cells (asexual reproduction), by far the most common method is that in which a male reproductive cell (*sperm*) unites with a female reproductive cell (*egg*) to form a *zygote*. This new cell, which is made up of cellular materials from both parents, undergoes successive divisions to form an *embryo*.

Regional differentiation of cells occurs in such a way that sheets of cells, the *primary germ layers*, are soon formed. In all except the least complex metazoa, three such germ layers are developed: the *ectoderm*, the *endoderm*, and the *mesoderm*. It is as though the embryo



Figure 7.5 *Amphioxus*, shown here about natural size. (The American Museum of Natural History.)

were both a weaver and a tailor charged with the task of making a suit of clothes. Before attempting to start the actual construction of the garment, it first weaves its cells into three kinds of "cloth." Thus, early embryogeny is concerned with cell division and differentiation to the extent that the primary germ layers are laid out and made available for more exact specialization of body parts. The details of this process differ somewhat among the various species of animals and especially among members of phyla which are widely separated in the phylogenetic scale. However, it is significant that this general plan of primary germ layer formation is seen wherever sexual reproduction occurs in multicellular animals.

As an example of the actual process of germ layer formation, let us consider the early development of an animal whose common name is amphioxus (Figure 7.5), a protochordate, which has been the subject of much study, and whose development is similar to that of both the vertebrates and many of the invertebrates. Amphioxus is a marine animal about two inches or less in length which spends most of its adult life buried in the sand of the shallow ocean floor with only the anterior end of its elongate body protruding into the water. Male and female individuals release their reproductive cells simultaneously in the same vicinity, and zygotes are soon formed as a result of sexual union of eggs and sperm.* Development of the zygotes and embryos proceeds on or near the surface of the water.

The egg of amphioxus is relatively small (about one-tenth of a millimeter in diameter) and contains very little stored food. Successive cleavages (Figure 7.6) produce a ball of cells which gradually round up to enclose a cavity (Figure 7.6f). At this point, the embryo is called a *blastula*, and the cavity is termed a *blastocoele* (Gr. *blastos*, sprout + *kolia*, cavity). When the blastula is fully formed, more than two hundred cells are arranged in a single thickness around the blastocoele. Each cell is referred to as a *blastomere*.

It will be noticed that the cells at one side of the blastula are larger than the rest (Figure 7.6e,f). This is a result of their being derived from that portion of the original cell which contained the most yolk, or stored food material. By the time blastulation is complete, these cells begin to lag behind the others in their divisions. This difference in division rates, plus certain other forces, causes an inpushing of these larger cells, much as though one were to push his finger into a soft, hollow rubber ball (Figure 7.6f-h). This changes the single-walled blastula to a double-walled form called a *gastrula*, and the point where the inpushing occurred marks the site of an opening, the *blastopore*, which opens into a new cavity, the *archen-*

* "Sperm" is both singular and plural.

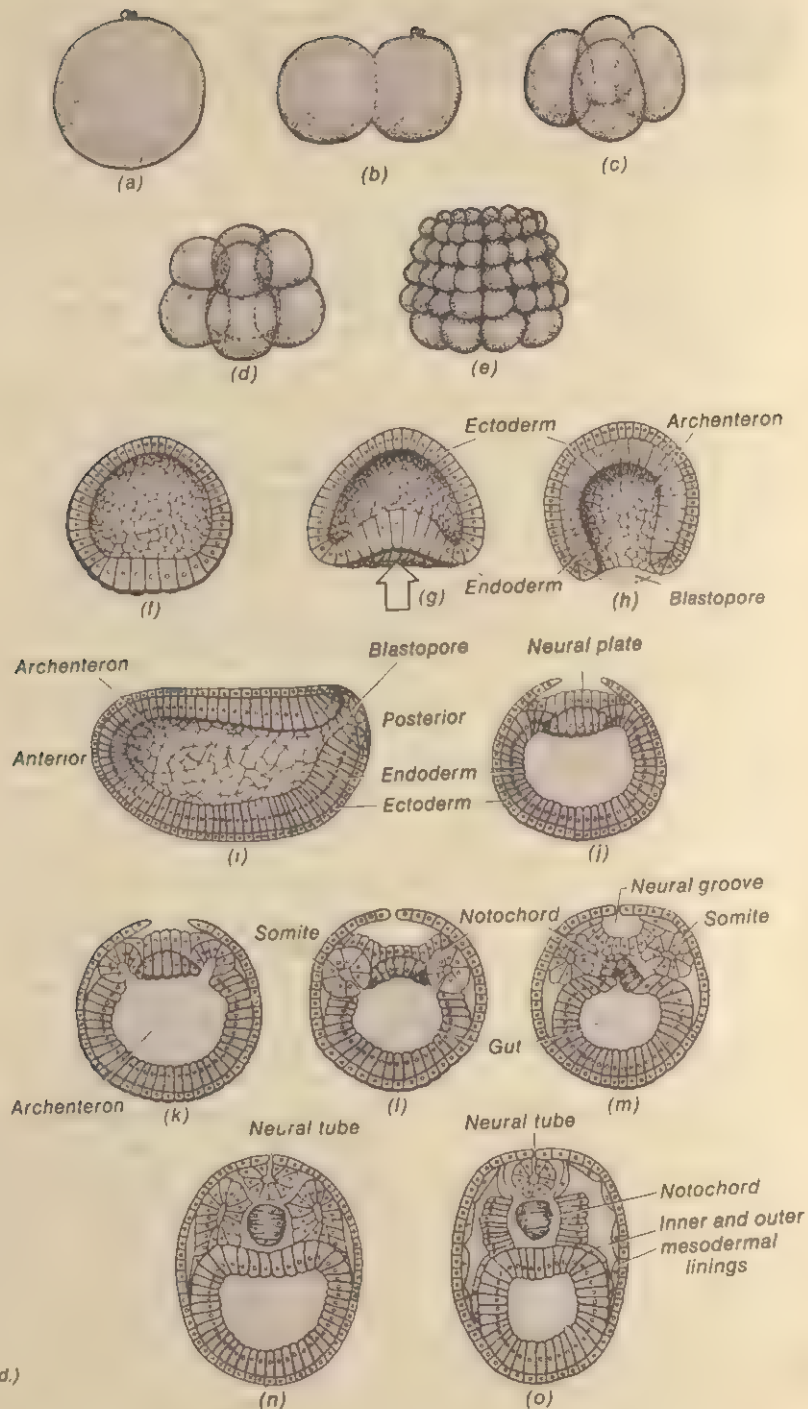


Figure 7.6 Developmental stages of amphioxus. At (h) during the gastrula stage, the embryo begins to elongate [see (i), which is shown in sagittal section]. Figures (j) through (o) represent transverse sections, hence their different appearance from (i). See text for further explanation. [Figures (a) through (e) used by permission from T. I. Storer and R. L. Usinger, *General Zoology* (4th ed.) (New York: McGraw-Hill Book Company, 1965). Figures (f) through (o) are from M. Sussman, after C. A. Villee, *Biology* (3rd ed.) (Philadelphia: W. B. Saunders Co., 1957).]

teron (the blastocoele having been obliterated by the inpushing of cells). Thus, the embryo at this point exhibits two layers of cells, the ectoderm and endoderm.

Further development results in an elongation of the embryo (Figure 7.6*r*) and an overlapping of the blastopore by the ectoderm. The dorsal surface becomes flattened, and the central portion of the ectoderm of that region begins to sink inward, pushing that part of the endoderm which lies beneath it into the archenteron (Figure 7.6*j*). This results in the formation of the neural tube, a structure which later gives rise to the entire nervous system from that portion of the ectoderm which sinks inward (Figure 7.6*k,l*). Endodermal cells,* affected by the movement of those cells which form the neural tube, give rise to the third germ layer, the mesoderm, which immediately begins the formation of a *somite* on each side (Figure 7.6*k,l*). Each of these elongates ventrally to encircle the gut, eventually meeting beneath it. Thus, a coelome is formed by an enlargement and fusion of the somites on each side of the embryo, and the mesodermal cells involved form the peritoneal coelomic lining. Meanwhile, certain mesodermal cells form the notochord, which lies just ventral to the neural canal (Figure 7.6*l-o*).

Since a full account of the development of amphioxus would take us farther into the field of specialized embryology than we can afford to go, we shall terminate our description of its development at this point. Suffice it to say that further differentiation of the primary germ layers and their derivatives results in the eventual development of body organs and systems. It is apparent, however, that early embryogeny proceeds in a definite and clear-cut manner to produce the three primary germ layers and to arrange them in such a way that later specialized tissue and organ formation can occur. Although development in other animals is varied in specific detail, with many individual differences being noted, that of amphioxus may be considered representative. To say the least, some pattern of germ layer formation is followed in the development of all multicellular animals, and perhaps the description of amphioxus embryogeny given above will at least serve to emphasize this point.

No doubt it would be of interest to the student to trace the development of the human embryo, but there are at least two factors which render such a study impracticable at this point, the first of which depends upon the fact that relatively little is known about early stages of human development, since it is extremely difficult to recover very early human embryos. Although a few have been stud-

*Technically, the inner layer at this stage is not *endoderm*, but *mesendoderm*, since it later gives rise to both endoderm and mesoderm.

ried closely, the field of human embryology has had to rely heavily upon studies of monkey embryos and the like, establishing by inference the stages through which the developing human passes. A second difficulty lies in the complexity of human (and general mammalian) development. Unless one has engaged in a phylogenetic study of embryology leading up to the mammal through the other classes of vertebrates, he is in a poor position to understand the events which occur and their significance.

In the multicellular animals whose body systems are well developed, the primary germ layers give rise to certain definite organs and organ systems. The ectoderm develops into the outer layer of the skin and also gives rise to the nervous system. From the endoderm are derived the inner lining of the gastro-intestinal tract and its associated organs. The mesoderm proves to be the most versatile of the three layers, that portion which is associated with the embryonic gut forms the outer wall of the gastro-intestinal tract and the outer

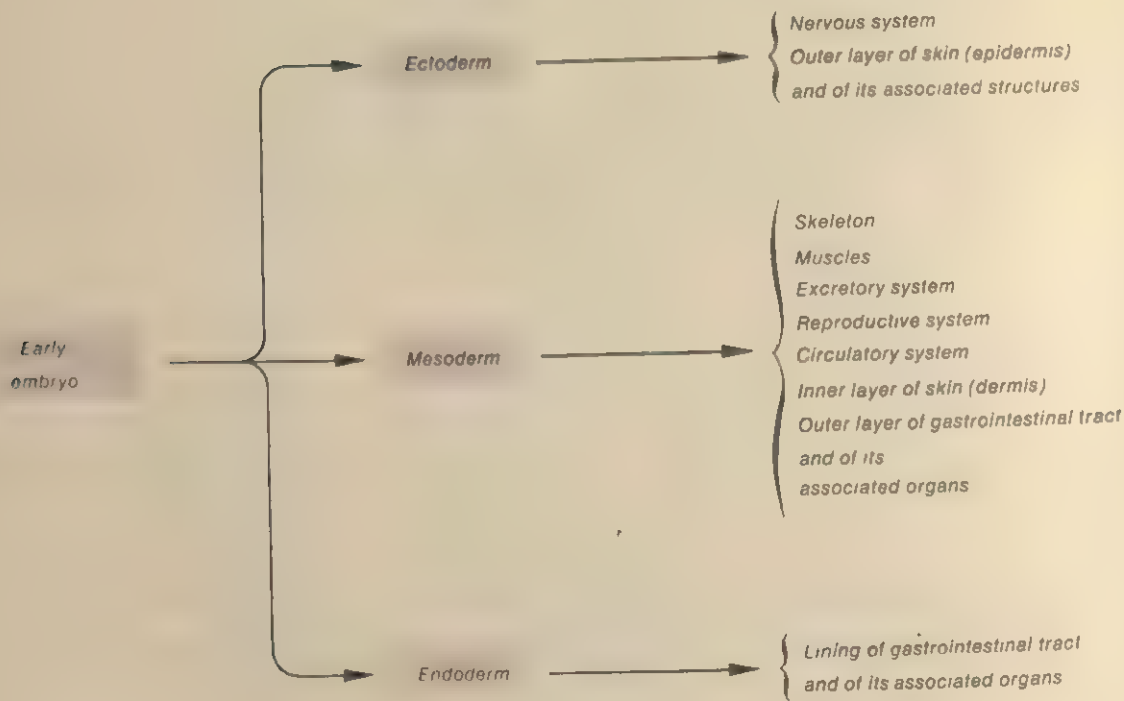


Figure 7.7 Important structures and organ systems of the vertebrate body according to germ-layer derivation

covering of organs which attach to it, while that part which lies next to the ectoderm gives rise to structures such as bones and muscles, and to the inner layer of the skin (Figure 7.7).

Tissue types of the higher animal body After development is well advanced and the many cells of the higher animal body have become in large part highly specialized, they tend to be associated together as tissues according to function. Four types of animal tissues are generally recognized by histologists. These are termed *epithelial*, *nervous*, *muscular*, and *connective*. Nervous tissue is derived entirely from ectoderm, muscle and connective tissue generally arise from mesoderm, and epithelium may come from ectoderm, mesoderm, or endoderm, depending upon its location in the body.

Epithelial tissue is essentially protective in its function, and it serves to cover or line surfaces. One is inclined to think only of the external body surface in this connection. The outermost layer or layers of cells are epithelial in multicellular animals, but a great many internal surfaces exist, and epithelium is also found as a protective tissue for these. The gastro-intestinal tract is lined in this fashion on its internal surface. The external surfaces of organs which lie within or adjacent to the body cavity of a given coelomate animal are covered by peritoneum, an epithelium of single cell thickness. Blood vessels and tubules of various sorts exhibit this characteristic also. Epithelium frequently assumes other roles in addition to that of protection. One of these is that of *secretion* in which certain epithelial cells produce some particular substance or substances, an aggregation of such specialized cells which perform a common secretory function is called a *gland*. Another secondary role played by epithelial cells is that of *absorption*, as is the case in cells which surround the lumen of the small intestine. We have already seen that in the movement of digested foods from the small intestine of man to the blood and lymph streams, they must be absorbed into the epithelium, a process which is in a sense, somewhat the reverse of secretion. Figure 7.8 illustrates representative epithelia which are found in higher animals.

It is the specialized function of nervous tissue to transmit impulses throughout the animal body. In their organization, nerve cells form a coordinated system which allows for the reception of external or internal stimuli, the transmission of impulses arising from such stimuli, and an orderly distribution of these impulses to organs of action. The typical nerve cell (Figure 7.9) is well adapted to this function, consisting as it does of a cell body whose cytoplasm may possibly extend for considerable distances in the form of *nerve fibers*. These fibers maintain connections with fibers of other nerve cells, and there is thus a systematic mechanism for reception, trans-

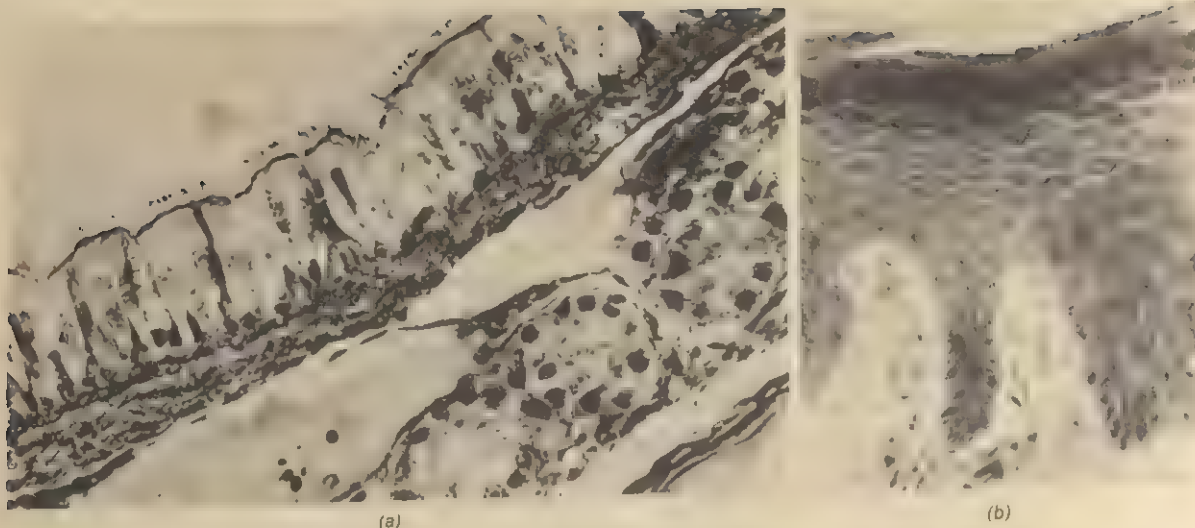


Figure 7.8 Two types of epithelial tissues (a) a section of the human trachea, showing a row of columnar cells whose outer surfaces are covered with cilia (Carolina Biological Supply Co.). (b) stratified, or layered, epithelial tissue as seen in the human skin. The upper portion is the epidermis which is epithelial, and the lower (light) portion is the dermis, which is composed of connective tissue.



Figure 7.9 Three large nerve cells from a thin slice taken through the spinal cord of an ox. Note the prominent nuclei and the several fibers that extend from each cell.

mission, and action. It is significant that nervous tissues are found in all multicellular animals except sponges, and that the morphology of nerve cells is remarkably uniform among the animals that possess them. The function of nervous tissue in higher animals will be considered in a later chapter.

Like nervous tissue, muscle is found in all multicellular animals except sponges. It is specialized for contraction, and the animal possessing it thus is able to exhibit a considerable degree of motility. Muscle cells are somewhat elongate, and contraction occurs when a complex series of chemical reactions within a given cell cause it to become shortened and thickened. In all but the least complex animals, many muscle cells may be bound together to form a *muscle*, in which case their contraction is very highly coordinated in the performance of work. In the vertebrates, three types of muscle cells are recognized. There are those which are *striated*, so called because small bands or striations are seen when the cell is highly magnified (Figure 7.10a), those which are *smooth*, lacking such striations (Figure 7.10b), and a third type are known as *cardiac* (Gr. *kardia*, heart) cells, which are found only in the heart (Figure 7.10c). Striated cells, or fibers, are usually fairly long and are multinucleate. They are associated with the endoskeleton in vertebrates, to which they attach



Figure 7.10 Types of muscular tissue: (a) a portion of a striated muscle fiber; (b) several smooth muscle fibers closely packed together; (c) cardiac muscle tissue—note branching of fibers and light striations. (General Biological Supply House, Inc.)

in groups as muscles. Smooth muscle cells are found in the internal organs, for example, in the wall of the gastro-intestinal tract. They are uninucleate, and contract much more slowly, as a rule, than do striated fibers. They may be grouped together in sheets or bands, or they may exist as somewhat isolated units. Cardiac muscle presents a rather complex, branching appearance, with individual cells lying alongside and across one another in close contact. Muscle cells or fibers usually contract through nerve-transmitted stimuli.

As the name implies, connective tissues serve chiefly to bind the other tissues together in the organism, although some are specialized for other functions, as is described below. One characteristic which all connective tissues share is that nonliving *fibers* are closely associated with cells, both of which are surrounded by a nonliving *matrix*. Both the fibers and the matrix are produced by the cells. Three general types of connective tissues are recognized by histologists, namely, *binding*, *supporting*, and *fluid* tissues. Binding tissue serves to connect the outer epithelium (epidermis) to underlying tissues such as muscle, it ties nerve fibers into bundles, and so on. Ligaments and tendons which connect bones to each other and to muscles, respectively, represent a type of binding connective tissue in which fibers are sufficiently numerous that they replace much of the matrix ordinarily present. Supporting tissue is represented in the higher vertebrates by bone in which the matrix becomes impregnated with calcium salts and is thus solid, and by cartilage, in which the matrix is less firm. It should be borne in mind that supporting tissues, although unusually compact, contain living cells which are continuously active in maintaining the fibers and matrix. In fluid connective tissues, of which the blood of vertebrates is most typical, the matrix exists as a liquid and fibers are only *potentially* present in the form of a blood protein called *fibrinogen*. Whenever blood is induced to clot through the initiation of certain complex reactions, fibrinogen is precipitated out of solution and fibers are formed. A blood clot consists of these fibers plus any blood cells that may become enmeshed in the fibrous network. The various types of blood cells represent the living portion of this fluid tissue. Representative connective tissues are shown in Figure 7.11.

The four types of tissue are bound together within the animal body in the formation of organs. The stomach, for example, is an organ whose wall is composed of two epithelial layers surrounding smooth muscle fibers. These layers, along with blood vessels and nerves, are held together by connective tissue. Even in an organ such as a muscle, where one type of tissue predominates, other tissues are present. Binding connective tissue ties the muscle cells together in this case, and nerve fibers supply them with impulses.

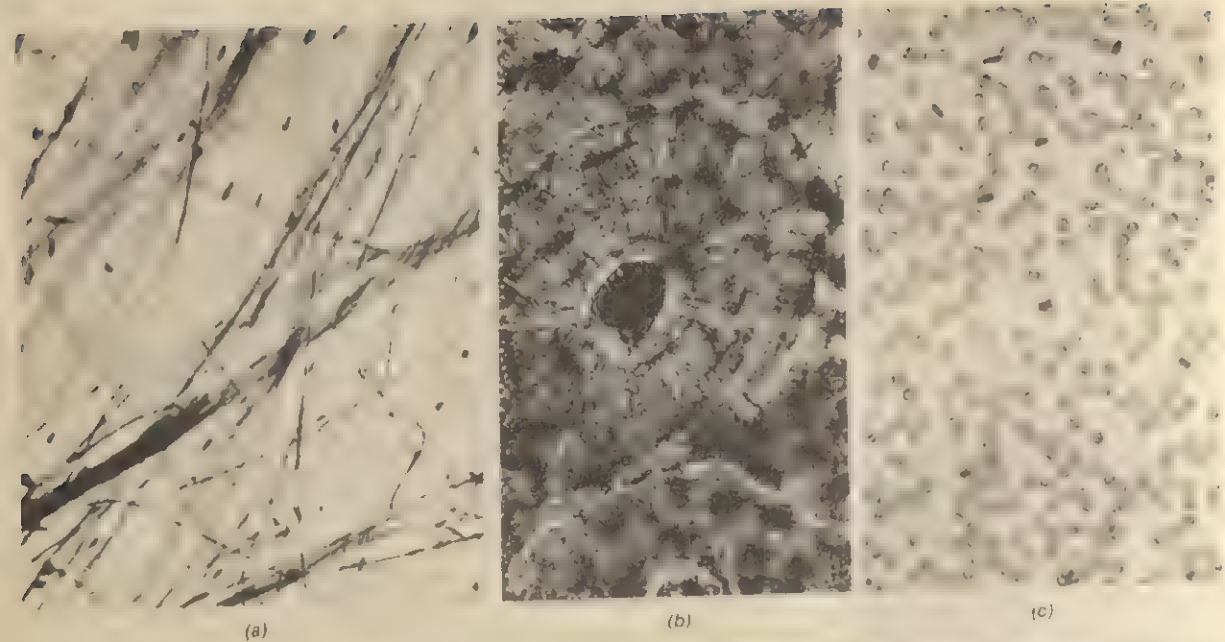


Figure 7.11 Some connective tissues. (a) one type of binding connective tissue—note fibers, among which are cells whose nuclei are stained darkly. (b) a thin section of human bone, showing characteristic circular arrangement of cells (very dark as shown here) within the firm matrix. (c) human blood in a stained preparation showing several red cells. (Carolina Biological Supply Co.)

7.5 Growth and differentiation in plants

Ontogeny of higher plant tissues It is rather obvious that plants and animals, especially those whose bodies are somewhat complex, are vastly different in their overall morphology. This is an accompaniment of their different modes of existence and simply reflects the principle that structure and function are closely related in organisms. Thus, the animal tissues that we have studied show adaptations to an actively motile type of organism whose body cells generally carry on a high rate of metabolism. A somewhat different picture presents itself when tissues of the complex plant are examined, however. These reflect the sedentary existence carried on by the plant, and adaptations to the structural and functional requirements of this mode of life become obvious with study.

Although certain nonvascular plants (for example, the giant kelps and the mushrooms) exhibit bodies of considerable size and complexity, as a general rule relatively little specialization is seen in their cells. It is particularly significant that they lack tissues which make possible the transport of fluids throughout the plant body. This necessitates a mode of existence for the plant which will enable

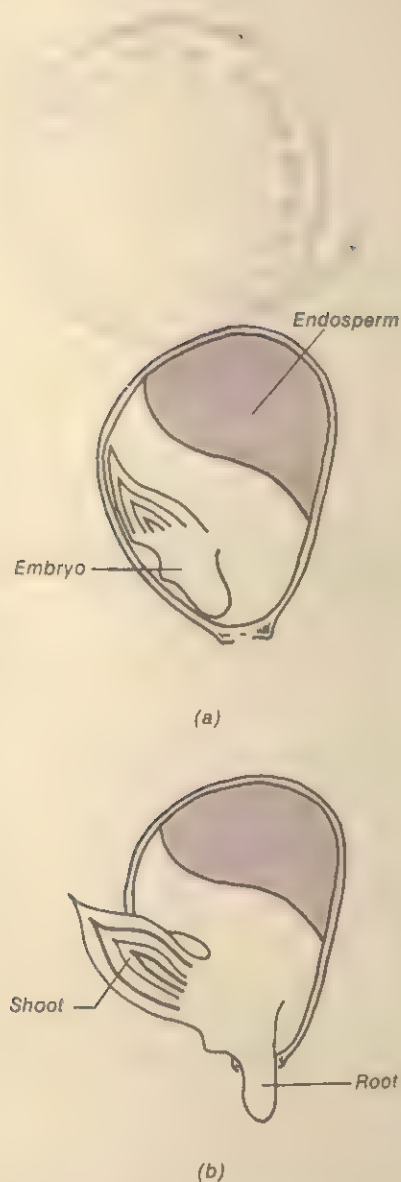


Figure 7.12 Diagram of seed germination. (a) dormant seed. (b) Germinating seed. Note emergence of root and shoot.

some of its cells to receive vital materials from other cells by diffusion. Thus, it is no accident that the nonvascular plants, except for certain algae whose cells are all in relatively close contact with nourishing seawater, do not usually attain much size since they are limited by their lack of specialized conducting tissues. Because the nonvascular plants demonstrate a limited degree of cellular differentiation, therefore, little value is to be gained in studying their development in the hope of discovering any great degree of histological specialization.

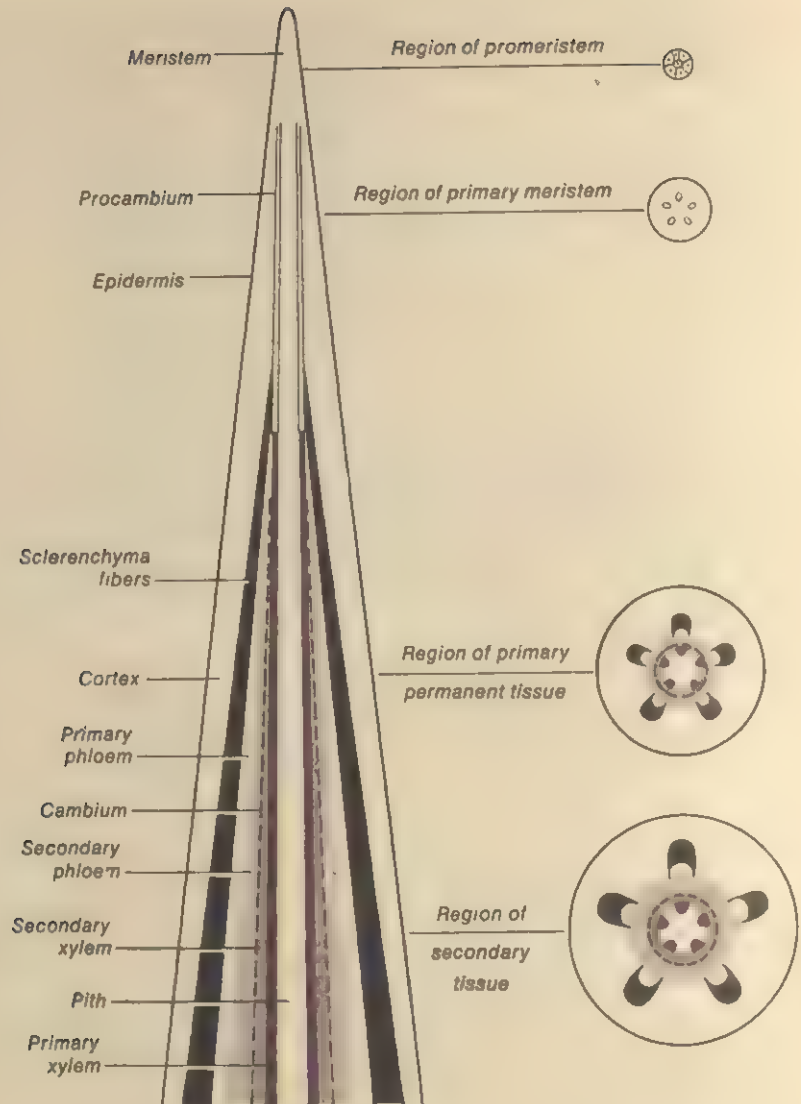
The vascular plants offer an entirely different picture, however. Not only does a high degree of cellular differentiation result in the presence of tissues that conduct fluids, but there are adaptations for greater size and more varied habitats. As is the case in animals, there is a considerable degree of variation in the structure of higher plants, but there are tissue types which are common to all.

Embryogeny of typical vascular plants begins with early divisions of the zygote within the tissues of a parent plant. Although there is little or no histological specialization at this point, a pair of embryonic organs, the *root* and the *shoot*, soon become evident (Figure 7.12). The root, which exhibits a positive response to gravity, ultimately gives rise to the root system of the plant, whereas the shoot, which is affected oppositely in its growth, serves as the forerunner of the *stem* and *leaves*. In the seed plants, the embryo usually stops growing just after these embryonic organs have developed and becomes surrounded by the tissues derived from the parent plant in the formation of the seed.* The seeds of many plants undergo a period of dormancy which seems to be an adaptation for propagation of the species. If seeds of a plant produced in the fall of the year in temperate climates were to germinate immediately, for example, they would all be killed by cold weather, and none would remain for spring germination. There are other species whose seeds remain dormant only until proper conditions of moisture, temperature, and oxygen supply are such as to initiate embryonic growth.

After the root and shoot have grown for a short time, some of their cells differentiate to form the tissues characteristic of the mature plant. Cells generally remain at about the same level of the plant organ where they begin to specialize. New growth occurs at the tip, which makes it possible to study the changes that take place simply by proceeding from the younger to the older cells. If one starts at the tip of a young shoot and proceeds downward by examining both transverse and longitudinal sections, he finds that the first cells encountered are small, undifferentiated cells which are active in

* Up to this point, the root and shoot are not influenced by gravity. It is after germination of the seed that their orientation with respect to this force begins.

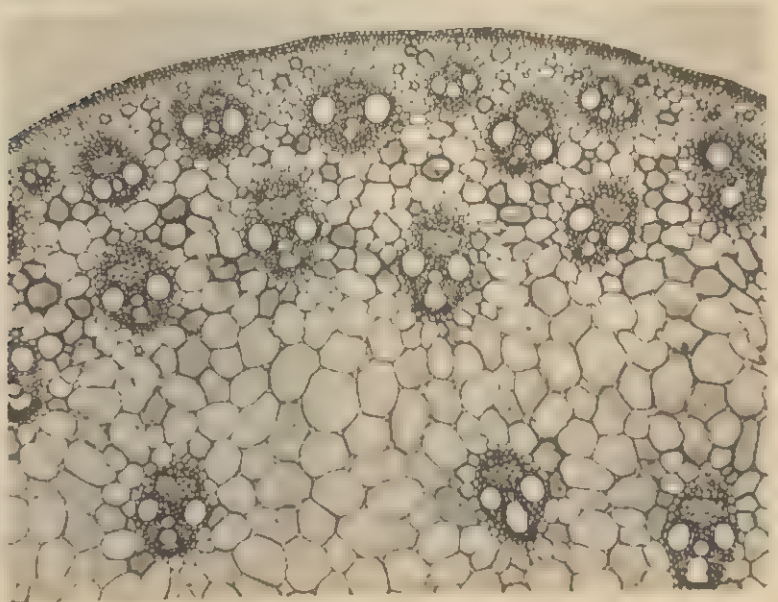
Figure 7.13 Diagrammatic representation of a stem tip, showing the development of tissues as a result of cellular differentiation.



division. These constitute *meristematic* tissue, a term applied to any tissue in a plant that possesses the ability to undergo active division. As more cells are produced by division, those that are older remain at the same level at which they were produced and begin the process of differentiation. Thus, as one proceeds farther and farther down the stem in his sectioning and study, successive degrees of specialization are seen. Figure 7.13 shows the result of making sections in this manner, with various levels of increasing complexity being identified.

Tissue types of the higher plant body As a consequence of gradual differentiation, certain tissues come to characterize the mature plant. For purposes of convenience, these may be classified as being either *simple* or *complex*, a distinction based on whether a tissue is composed of one cell type or several cell types. Near the growing tip of a given plant organ, one of the first simple tissues to become differentiated is *epidermis*, which persists as an external layer, usually one cell thick. It is essentially a protective tissue, and chloroplasts are often absent in all its cells except guard cells. The most common simple tissue to be found in higher plants is *parenchyma*, cells of which serve chiefly in synthesis or storage. They are rather thin-walled, usually exhibiting only slight elongation, and function in the living state (Figures 7.14, 7.15). Another simple tissue is *collenchyma*, which is concentrated chiefly at sites in the plant where strength and support are required while the plant is still relatively young. These cells generally possess rather thick walls composed of cellulose and they tend to become somewhat elongate (Figure 7.15). Like parenchyma, they function as living cells. A fourth type of simple tissue is *sclerenchyma*, cells of which assume two different forms. Some are isodiametric (such as the *stone cells* which lend a gritty aspect to the edible portion of a pear) and others may become extremely elongate, the latter being called *fibers* (Figures 7.15, 7.16). Unlike the preceding types of simple tissue, sclerenchymatous cells do not achieve their full potential function until after their proto-

Figure 7.14 A portion of corn stem (monocotyledonous) in cross section. Note scattered vascular bundles, each of which resembles a "face." In each face, the eyes are large xylem vessels, the forehead is phloem, with companion cells appearing small and square in this view, sieve tubes larger and more rounded. Large storage cells of parenchyma are located between the vascular bundles. (General Biological Supply House, Inc.)



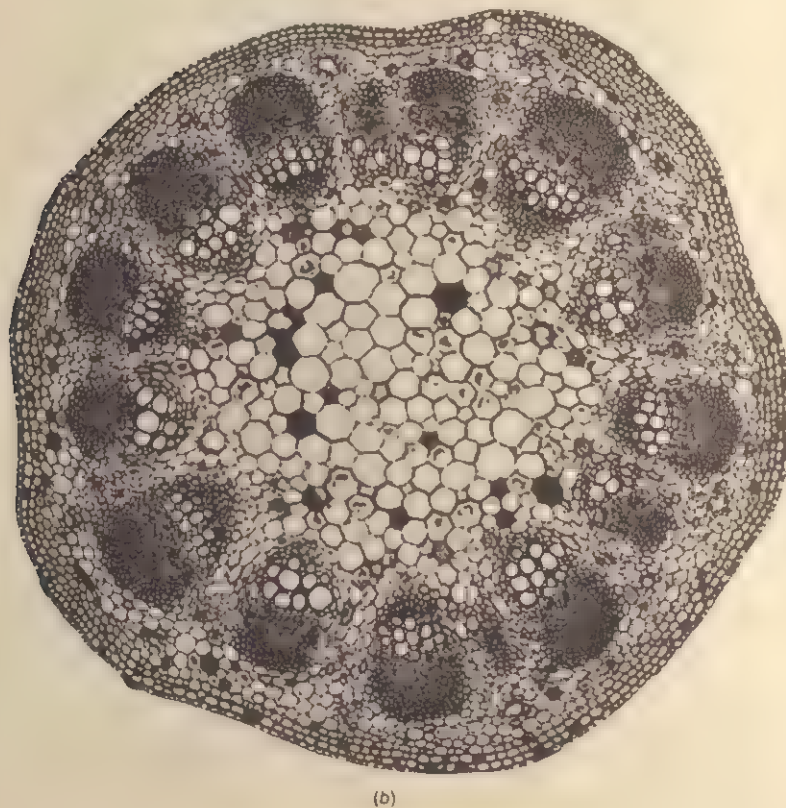
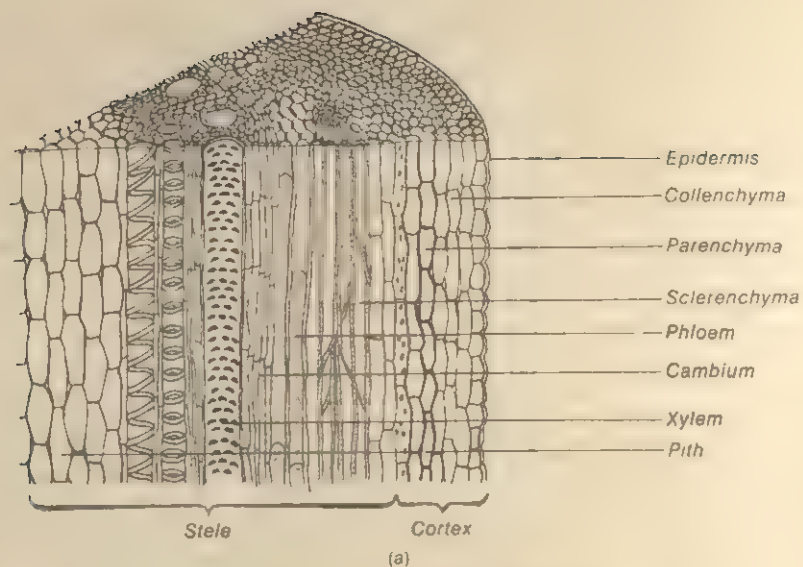
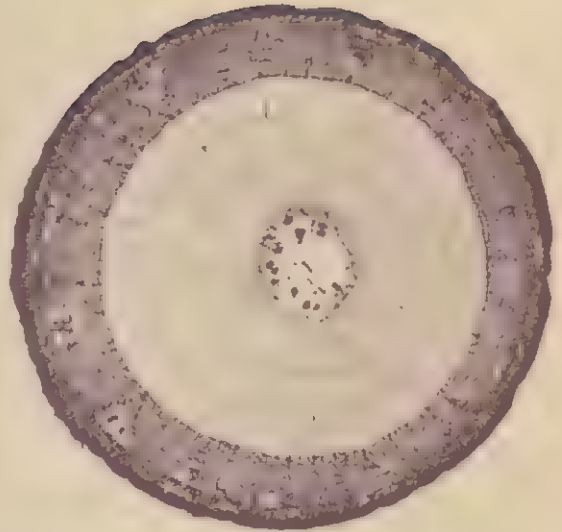


Figure 7.15 (a) Three-dimensional representation of a herbaceous stem, showing a portion of a vascular bundle. Note the relationship of several types of tissue within the stem. (b) Cross section of a herbaceous stem (sunflower), showing epidermis, cortex, and stele. Note the circle of vascular bundles, each composed of xylem, phloem, and cambium. The large (parenchymatous) cells occupying the central portion of the stem constitute the pith. (Carolina Biological Supply Co.)

Figure 7.16 Cross section of a woody stem (basswood) in its third year of growth. The dark outer area is the bark, and it is separated from the lighter area (wood, or xylem) by the cambium. Note the annual growth rings in the xylem. The innermost area is the pith, which is somewhat crushed owing to pressures exerted upon it by the centrifugal growth of the stem. (Carolina Biological Supply Co.)



plasts have disappeared, a process which leaves an extremely thick cell wall surrounding a small *lumen* formerly occupied by the protoplasmic contents. The walls of sclerenchymatous cells owe much of their strength to a material called *lignin*, which becomes associated with the cellulose of young cell walls as they gradually differentiate. This physical characteristic renders sclerenchyma, and especially fibers, very serviceable in lending strength to a given plant part. The fibers of some plants such as flax and sisal are commercially valuable since they can be used in the manufacture of such commodities as cloth and ropes. In addition to these four types of simple tissues, it should be remembered that meristem is always present at the growing tips of plant organs, as well as at various other locations in the plant, and it may be regarded as a *fifth type*.

Complex tissues are of two types, *xylem* and *phloem*, which are concerned with the movement of materials in vascular plants. The functional cells of xylem are either elongate, somewhat tapering units called *tracheids* (Figures 4.35, 7.16), whose ends join in the function of conduction, or *vessel elements*, which are larger and more uniform, and which become fused together at their ends to form conducting tubes called *vessels* (Figures 4.35, 7.14–7.16). The walls of tracheids and vessels, like those of sclerenchymatous cells, are characterized by the presence of *lignin*, which lends great strength to them. Lignin may be deposited in the walls of these cells according to a variety of patterns, namely, as rings, spirals, networks, and so on. These conducting cells of xylem lose their protoplasts upon reaching maturity, and the fluids which they conduct travel

through the region of each cell originally occupied by living material. In addition to the tracheids and vessels that have been described, parenchyma cells and sclerenchymatous fibers often are present in xylem, the entire aggregation of cells associated together in the common function of fluid transport being regarded as a single tissue type. In general, xylem serves to transport water and dissolved materials upward in the plant. The functional units of phloem are called *sieve cells*, and they are somewhat analogous to the vessel elements of xylem: in many plants, sieve cells are formed as multicellular tubes comparable to xylem vessels. Unlike the latter, however, they retain their protoplasm in the functional state, although nuclei disappear. Typically, sieve cells are very closely associated with other components of phloem called *companion cells* (Figures 4.35, 7.14). Because there are perforations between companion cells and sieve cells, it has been suggested that the nuclei of the former may serve the cytoplasm of the latter. In addition to these two cell types, phloem is always characterized by the presence of *phloem parenchyma* and frequently by sclerenchymatous *phloem fibers*. In the transport of fluids, which are chiefly dissolved food materials manufactured in the upper parts of the plant and which are carried downward to other parts, the sieve tubes perform a similar function to that of tracheids and vessels in regard to the movement of materials upward in the plant.

Distribution of these tissues throughout roots, stems, and leaves varies greatly among plants, but there are some definite structural patterns that can be identified. Xylem and phloem tend to develop centrally in roots with absorption occurring only at the level of the root where epidermal *root hairs* are present (Figure 7.17). Water and dissolved inorganic salts pass into the root hairs, and from cell to cell inward toward the xylem, by way of which these materials travel upward in the plant. Sectioning of the roots of flowering plants at the region where they join the stem reveals the phenomenon that xylem and phloem become dispersed from their central position and form isolated areas known as *vascular bundles*. These bundles are characteristically arranged in a circular pattern in dicotyledonous plant stems, whereas in many monocotyledonous stems they tend to occur randomly (Figure 7.14). Roots and stems exhibit three general regions, called *epidermis*, *cortex*, and *stele*. The epidermis (which is a tissue as well as a region) is typically a single layer of cells, the cortex is that region extending from the epidermis to the beginning of vascular tissues, and the stele is composed of all cells which are thus surrounded by the cortex (Figure 7.15). The stele of many roots forms a solid, central cylinder without pith, and the cortex of the root

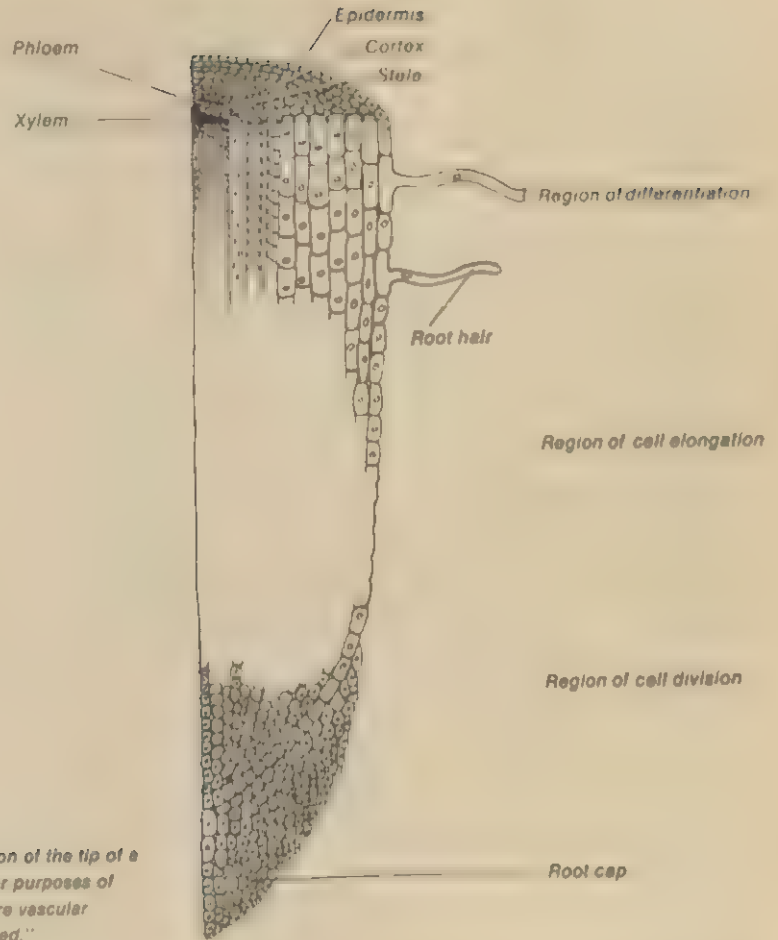


Figure 7.17 Three-dimensional representation of the tip of a young root, shown in longitudinal section. For purposes of illustration, the region of differentiation, where vascular tissues begin to form, is somewhat "telescoped."

is relatively more expansive than that of the stem (Figures 7.14, 7.15, 7.17). Wherever a leaf grows from a stem, a vascular bundle gives off a *leaf trace* containing xylem and phloem, which serves the blade of the leaf by branching into *veins*.

Thus far, we have spoken of meristem only in terms of its presence at the tips of growing plant organs, but wherever growth occurs in the plant, it must do so by virtue of cells which are functionally meristematic. Again, there is considerable variation among plants in this regard, and it is difficult to establish generalizations regarding plant growth. In tree-like and shrubby seed plants, areas of meristem called *cambium* develop between the xylem and phloem of stems

and roots. In the stem of this plant type, for example, the xylem and phloem of each vascular bundle is separated by cambium (Figure 7.15). Division of this layer results in more xylem and phloem, since cells produced by the cambium may become associated with either tissue. As the stem continues its development, the layer of cambium grows in such a way as to form a complete circular sheath, and thus an increase in stem diameter is made possible by constant division of the cambial cells. Stems of woody plants exhibit a cambium which adds zones of xylem and phloem annually. A plant stem of this type grows laterally in such a way that the original xylem is buried along with the pith. Just outward from the cambium, phloem continues to be produced, and this plus other tissues (the original epidermis, cortex, and a meristematic layer called *cork cambium* with its derivatives) compose the *bark* of the perennial dicotyledonous stem. Hence the cambium is the point of separation between the bark and the xylem, which is also called *wood* (Figure 7.16).

7.6 Planarian worms (Figure 4.9), which are commonly found on the surfaces of rocks in ponds or streams, may be used for a simple and extremely interesting experiment in animal growth. It is possible to cut a worm in a variety of ways in order to produce the effect described below, but let us suppose that three transverse cuts are made in such a manner that four pieces are produced (Figure 7.18). This action not only fails to kill the worm, but if each piece is placed in a separate container of pond water, it grows into a new individual. This process of growth in the development of an entire organism from a part or in the regrowth of a lost or injured portion is termed *regeneration*. The growth and differentiation which are necessary in producing a new worm do not occur in a haphazard fashion; careful observation will reveal that an anterior end always develops from the portion of a given segment which lay nearest the anterior end of the

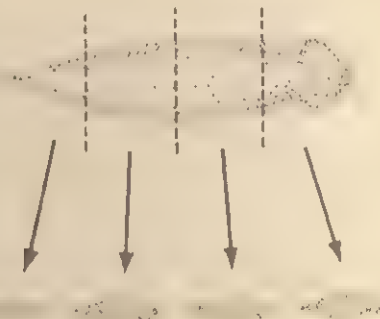


Figure 7.18 Regeneration in planaria, showing orientation along an axis so that a new anterior end develops from the anteriormost portion of the piece as it was situated in the original worm.

original worm (Figure 7.18). This implies a certain organization for growth on the part of the animal, apparently built around its longitudinal axis.

In general, the power of regeneration is great among those animals whose bodies are relatively simple and becomes more and more limited with the increase of complexity. Among the vertebrates it is virtually limited to the healing of wounds, a process that is extremely complex and not always completely successful, particularly when muscular and nervous tissues are destroyed. This differential in regenerative powers is obviously a reflection of the greater specialization seen in mature cells of the higher animal body: cells such as those of planaria are considerably more unspecialized and versatile than are most cells of the human adult, for example.

Although botanists usually prefer the expression "vegetative growth" in speaking of regenerative processes, plants also demonstrate the ability (in varying degrees) to replace and repair*. In fact, even some very complex plants may be propagated because of the tendency of their stems, roots, or leaves to develop into entire plants. Here again, as in planaria, there is generally an orientation. A piece of willow stem, for example, if placed in water, does not develop roots on the end that grew uppermost in the original plant even if this end is placed downward in the water; instead, roots grow at the lowermost end of the piece, if they grow at all, while leaves develop at the opposite end.

Perhaps the most important biological principle to be derived from experiments in regeneration is that plants and animals possess a certain organization above the cellular level which results in their being more than a mere sum of their parts, or cells. We have already seen that this is true in the development of animal embryos where the activities of cell groups called organizers have been clearly demonstrated in embryological research. To return to our former analogy, these organizers (both in embryos and in mature organisms) are comparable to civic clubs and other organizations within a society whose effects on that society supersede the influence of any one individual. Because of the extremely important principles and implications involved, both to biology and to philosophy, the area of research dealing with regeneration and organization is one of the most active and exciting fields of modern biological research.

* One reason the term regeneration is avoided by some botanists is that the term of individual plants tends to vary much more widely than it does that of animals. If a limb is broken from a tree, it is not replaced as such; the leaves that appear in the spring on a deciduous tree do not grow in the same positions occupied by the leaves that fell during the preceding autumn. Hence there is some justification for regarding plant regeneration as being fundamentally different, at least in an organizational sense, from that occurring in animals.

7.7 Growth means increase in mass, and it is made possible in living systems by the prevalence of anabolic processes over catabolic ones. For the most part, multicellular organisms grow by an increase in cell number. In their divisional processes, cells grow to a certain size and then undergo mitosis and cytokinesis. At some stage of development, a given cell of a complex organism may begin the process of differentiation toward a specialized form and function. The forces which are operative in differentiation are very poorly understood, although biologists are able to approach the problem through various hypothetical models.

In the more complex animal body, differentiation results in the development of four basic kinds of tissues: nervous, muscular, epithelial, and connective. Each of these tissues is represented by various structural types, each of which reflects to some degree the function to which it is adapted. In the more complex plant body, differentiation results in the development of several tissue types which may be classified as simple (those consisting of a single cell type) and complex (those consisting of more than one cell type). The major simple plant tissues are meristem, epidermis, parenchyma, collenchyma, and sclerenchyma. The two types of complex plant tissues are xylem and phloem. A special phenomenon of growth is regeneration, the capacity for which is more marked in those animals whose tissues are relatively unspecialized than in more complex forms. Among plants, the capacity for regeneration is fairly high at all levels of organization.

- Questions**
- 1 Summarize the process of cell division, contrasting important differences between plant and animal cells in this respect.
 - 2 What do you understand to be the meaning of the terms "histological specialization" and "cytological specialization"?
 - 3 Consider Spiegelman's definition of histological differentiation as "the controlled production of different enzyme patterns." How are genes *and* cytoplasm both involved in this process?
 - 4 Generally speaking, regenerative capacity is most pronounced in the less complex animals and, in a rather nonspecific sense, in plants. Can you advance a possible explanation for this? In planaria, what explanation might be offered for the orientation which occurs in regeneration?
 - 5 Fruit growers have hit upon a neat trick for producing prize specimens. For example, if a ring of the bark is removed from the lower part of an apple tree branch (a process called "girdling"), and

all the apples are picked off except one or two, these specimens may attain a phenomenal size. Can you explain this?

6 As a rule, cells which are engaged in active division are more susceptible to adverse conditions than cells which are in an extended interphase. For example, bacterial cells of a given strain are more easily killed by chemicals or heat when they are actively dividing than when they are not. The same principle is utilized in the destruction of cancerous cells of the complex animal body (which are usually very active in division) by X rays, if the dosage is regulated carefully, it is possible to destroy cancerous cells without damaging nondividing cells in the same area of the body. Offer a possible explanation for this phenomenon.

7 Would it be easier to study the ontogeny of the human or of a given species of pine? List some problems in each case.

8 Describe the location and function of cambium in a woody plant stem. Where is the *oldest* xylem located in such a stem? The *youngest* phloem?

9 Which of the three primary germ layers of the chordate embryo is most versatile with regard to the number and variety of tissues which are derived from it? Describe the early formation of the following as shown in amphioxus: nervous system, notochord, gut, mesodermal linings of the coelome.

10 Do all organisms grow? Explain.

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Reproduction

Organisms are relatively short-lived. When one considers that few animals present on the earth today live longer than 150 years (certain tortoises are known to live that long), this period of time seems small indeed when compared with the time that life has existed on our planet (probably over 2 billion years). Even the oldest known living plants, the bristle-cone pines (*Pinus aristata*), some of which are well over 4,000 years old, make a very slight impression upon the time scale. To draw a comparison, if the period of time that life may have occupied the earth were reduced to twenty-four hours, and the life span of the bristle-cone pine were reduced accordingly, the latter would be only about one-sixth of a second!

Because individual organisms do not live for a very long time, it is obvious that reproduction is the only mechanism whereby a species can maintain itself in time. As we have already observed (and this idea will be developed more fully in a later chapter), even species are subject to changes. Nevertheless, whatever stability is achieved in nature depends upon the ability of organisms to produce other organisms whose characteristics are essentially like their own.

This is not to say that all individual organisms reproduce. Circumstances frequently dictate that plants or animals fail to survive to a reproductive age, or possessing the full potentiality, are somehow unable to fulfill it. A puff ball, for example, may produce several million spores, but if none of them lodges on a suitable substratum, the puff ball has failed to reproduce itself. A single willow tree, isolated from others of its species, may not form seeds because of its dependence upon other trees for pollen. Many human beings live out their lives without producing offspring. Some organisms, for one reason or another, are sterile (lacking reproductive capacity) and therefore have no part in maintaining their species. Thus, when biologists speak of reproduction as a characteristic of living systems, the concept is not necessarily applied to individual organisms. Rather, it emphasizes the protoplasmic capacity to make more of itself from nonliving antecedents, and this ability may find expression at all organizational levels.

Let us make one additional observation with regard to the biological significance of reproduction. We have already seen that living organisms represent a dynamic state, that is, they are characterized by homeostatic mechanisms which wage a constant fight against chemical equilibrium. As we have mentioned previously, this is a battle that the individual organism never wins. When it is young and vigorous, an organism wages a very successful campaign in terms of metabolism and growth. In time, its versatility becomes lowered, and an aging organism survives only in the sense that it passes a part of itself on to succeeding generations. This part, whatever its form, contains instructions for making the "weapons" which are essential to its offspring for maintaining the steady state. This property of

protoplasm, which is exhibited in somewhat different ways at different levels of organization, is what we mean by reproduction. Organisms being what they are, this characteristic makes possible the continuation of the species. Furthermore, reproduction ensures the replacement of old organisms by new ones in a continuous chain, which tends to maintain biochemical and differential activities at a peak of effectiveness.

8.1 Sexual and asexual reproduction

Organisms exhibit a variety of patterns relative to reproduction, and different points of view may be taken with regard to classification of these patterns. For our purposes, we shall consider that there are two basic types of reproduction, *sexual* and *asexual*. Sexual reproduction is always associated with a type of nuclear division called *meiosis* which occurs at some point in the life cycle of the organism involved. Meiosis is discussed in a later section of this chapter. Furthermore, except for a few atypical cases, sexual reproduction is characterized by the union of *gametes*, or specialized reproductive cells, in the formation of a new individual. Such gametic union is followed by the fusion of the gametic nuclei and the association of their chromosomes; this entire sequence of events is known as *fertilization*. The two most significant features of sexual reproduction, at least in terms of our emphasis in this chapter, are meiosis and chromosomal association, mostly because of their genetic implications. It is sufficient for our purposes to regard any process in which there is the production of organisms without the formation of new chromosomal associations as asexual reproduction.

The vast majority of organisms exhibit sexuality, a phenomenon

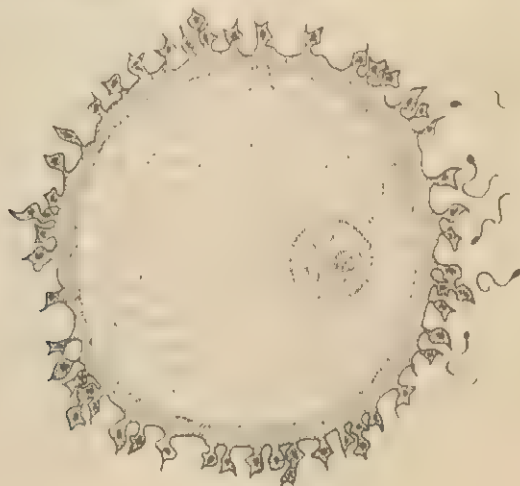


Figure 8.1 Human egg and sperm shown in relative size, enlarged about 500 times.

which, in its most obvious form, becomes apparent in the existence of two sexually distinct "kinds" of individuals (male and female) within a species. For purposes of definition, male and female individuals are distinguished from one another on the basis of their production of specialized reproductive cells, or gametes. Typically, the two cells which meet and unite in sexual reproduction are morphologically dissimilar, one being relatively large and non-motile, the other being relatively small and motile (Figure 8.1). When this is the case, the larger gamete is termed an *egg* or *ovum*, and the smaller one is called a *sperm*. Whenever an individual is capable of producing sperm it is designated a male; if it produces eggs, it is a female.

The major exceptions to this typical manifestation of sexuality are extremely interesting. Among several of the algae and fungi, there are two sexually distinct strains within a species that are morphologically indistinguishable in every detail. Sexual reproduction is carried on through the union of gametes, but there is no discernible structural difference between them. Because there is no basis for designating one of the strains "male" and the other "female," it is common to refer to one as the "plus" strain and the other as the "minus" strain in a completely arbitrary manner. Figure 8.2 illustrates

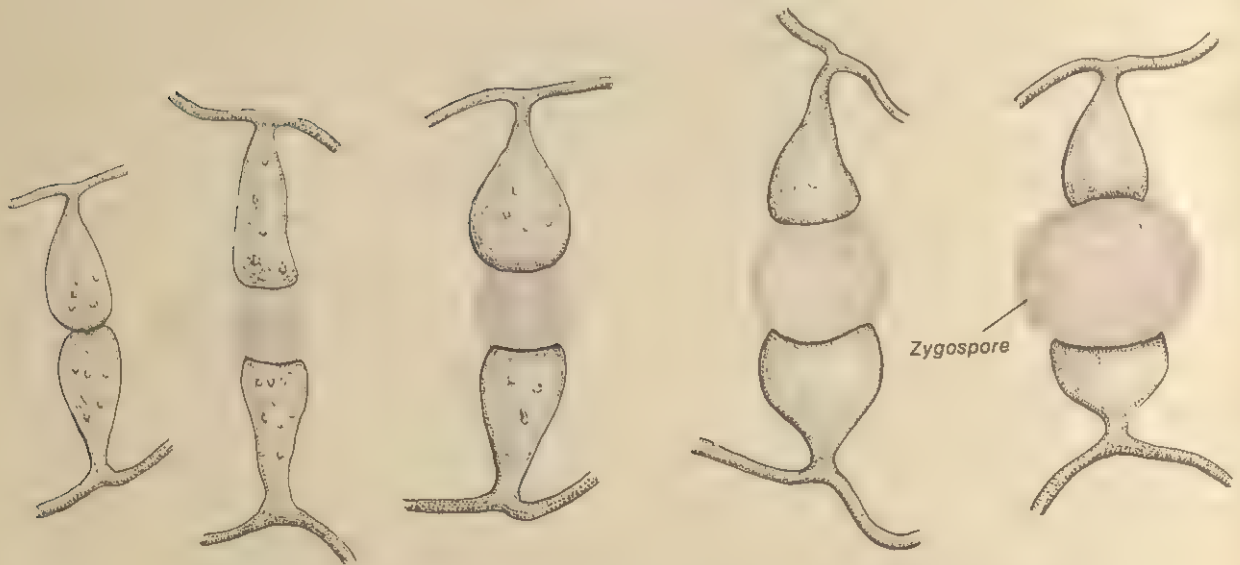


Figure 8.2 Sexual reproduction in a mold, *Rhizopus stolonifer* (see Figure 4.29). When "plus" and "minus" strains grow in the vicinity of each other, extensions of two filaments meet, an area of cytoplasm including several nuclei is delimited, and a thick-walled zygospore is formed. The zygospore, which is a product of sexual reproduction, may later germinate and form a new mycelium.

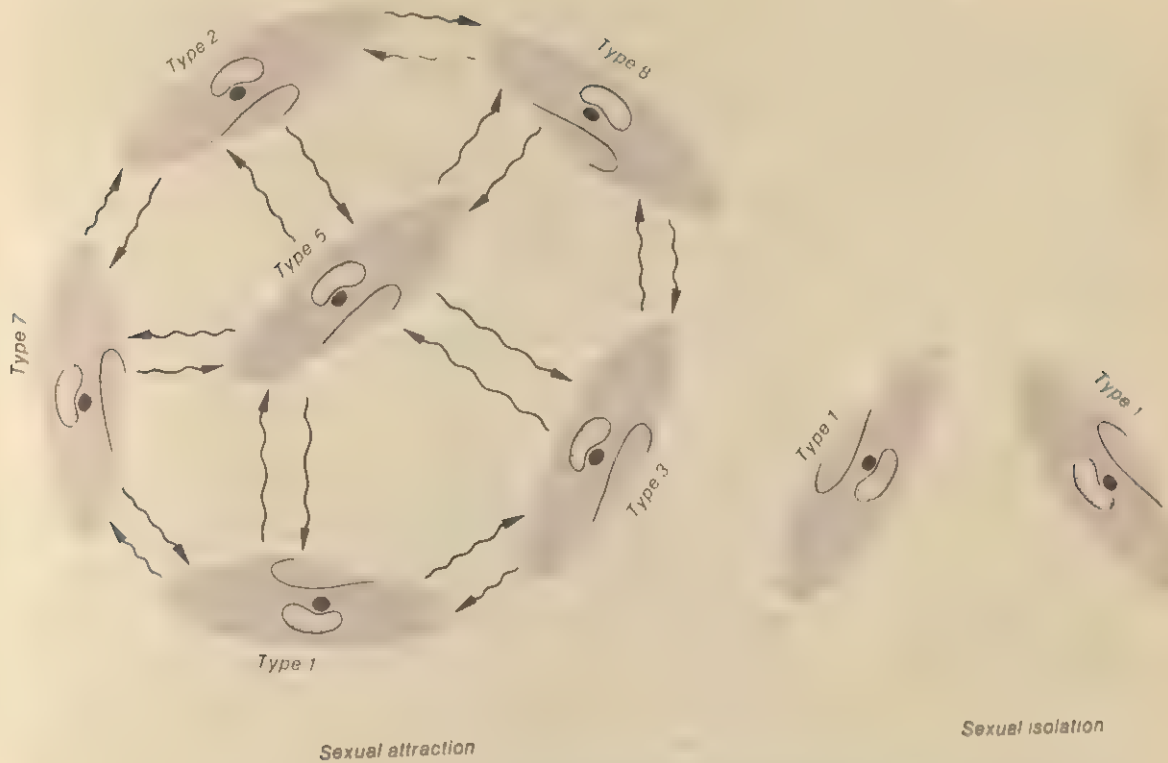


Figure 8.3 Multiple sexuality in *Paramecium bursaria*, one strain of which is known to consist of at least eight mating types. Each type will conjugate with any other, but not with members of its own type.

this type of reproduction as it occurs in a common mold. Certain protozoa exhibit a phenomenon called *multiple sexuality*, in which there are various levels of sex rather than two contrasting forms or strains (Figure 8.3). In multiple sexuality, the concepts of maleness and femaleness are, of course, entirely without meaning. Although most species of animals are *dioecious* (consisting of male and female individuals), some are *monoecious* (consisting of individuals which are functionally both male and female). In general, the most complex animals are dioecious, whereas the monoecious condition is limited to the less complex forms. An individual member of a monoecious species is called a *hermaphrodite* (Gr. *hermaphrodites*, from the myth of Hermaphroditus). The common earthworm is such an animal. It is interesting to note that in dioecious species an individual may occasionally be seen which possesses certain characteristics of both sexes. Such an individual is called a *pseudohermaphrodite*.

Such an individual is not functional both as a male and a female as is a true hermaphrodite, and its appearance in the species is considered abnormal. In plants, sexuality is generally obscured to such a degree as to render it virtually unknown to the casual observer. Nevertheless, most plant species feature sexual reproduction. In contrast to the situation among animals, the more complex plant species tend to be monoecious rather than dioecious, although these terms have a slightly different meaning in botany.

In dioecious organisms, cross fertilization occurs of necessity. However, in monoecious organisms, a possibility exists for self-fertilization. This is seldom realized in monoecious animals, because most hermaphrodites produce eggs and sperm at different times. In monoecious plants, self-fertilization is common, but even so, cross-fertilization is the rule.

Few species fail to exhibit sexuality in some form, but in spite of this, asexual reproduction is very widespread in the world of life. Many organisms reproduce most of the time in this manner, with sexual reproduction occurring rarely or occasionally. In general, asexual reproduction is limited in the animal kingdom to certain members of the lowest phyla in the scale of complexity, notably the Protozoa, Porifera, Cnidaria, and Platyhelminthes, of the phyla we have considered as major ones. In the plant kingdom, however, some of the most advanced plants reproduce in this fashion with regularity.

Fundamentally, there are two ways in which asexual reproduction may occur. The first method might be termed *somatic* (Gr. *soma*, body) *reproduction*, the essence of which is the production of a new individual from a part of the parental body. This form of reproduction involves more than a single cell whenever it occurs in multicellular organisms. The simplest form of somatic reproduction is seen in unicellular organisms such as protozoa, yeasts, bacteria, and certain algae whose cell division automatically results in their reproduction. We have mentioned previously that some organisms such as *Hydra* produce *buds* which ultimately develop into independent organisms. Certain of the free-living flatworms undergo a longitudinal division of the body, which results in the formation of two organisms from one. Among the more complex plants, some species exhibit very elaborate modifications for somatic reproduction, such as the tubers of Irish potatoes, the runners of strawberries, and the bulbs of tulips. As a second asexual method, some organisms exhibit the production of *spores*, which are single-celled units capable of growing into whole organisms. This method of reproduction is virtually limited to the plant kingdom, where it is demonstrated in some form by the vast majority of species.

Perhaps it will occur to the thoughtful student to wonder whether

or not regeneration, which was discussed in the preceding chapter, constitutes a form of asexual reproduction. In consideration of this question, it must be remembered that we limited the definition of this phenomenon to situations where parts of an organism are lost and replaced, or to those in which an entire organism develops from a part. Replacement of structures certainly does not constitute reproduction, nor can regeneration be considered a natural means of reproduction among organisms. We can separate a planarian worm into several parts experimentally and *induce* the regeneration of new individuals, but the worm does not perform this task autonomously. Hence, it is best to regard the term regeneration as one describing a certain aspect of growth. To state the matter another way, *growth and reproduction are two distinct phenomena*.

It should not be thought that sexual and asexual reproduction are necessarily exclusive in a given species. Although sexuality has never been observed in some species (for example, members of the blue-green algae apparently reproduce exclusively by asexual means), and in others reproduction is entirely sexual (as is the case with most animals), a great many species exhibit both sexual and asexual reproduction. *Hydra* (Figure 4.6), a common freshwater cnidarian, is such an organism. In addition to egg and sperm formation, which is a manifestation of sexuality, *buds* are frequently formed, and these eventually develop into adult individuals. Many flowering plants may be propagated from a root, stem, or leaf. This represents purely asexual reproduction, even though seeds may be formed as a *result of sexual reproduction*.

In comparing sexual and asexual reproduction in living organisms it might seem that asexual reproduction would have a number of advantages over sexual reproduction. An aquatic environment is frequently necessary for sexual reproduction to take place, particularly in such animals as *hydra* and most fishes where there is no direct contact between male and female individuals. In addition, the fusion of gametes is usually dependent upon the random movement of one of the gametic types (sperm). When sperm fail to make contact with eggs, the reproductive process is thwarted. Although a number of hazards are inherent in sexual reproduction, it has become the dominant form of reproduction among organisms. Perhaps there is some significance in this.

Earlier, we introduced the idea that chromosomes with their genes play an important role as intrinsic developmental factors and in the control of metabolism at all growth levels. It should be apparent that whatever part genes play in the development and in the homeostasis of an organism, these effects must of necessity remain unchanged from parent to offspring in asexual reproduction. This

principle has been exploited by man in the asexual propagation of many plants such as fruit trees when it is desirable to ensure that all qualities of a parent plant are exactly reproduced in the offspring, and here, this reproductive feature is of distinct advantage (to man). On the other hand, it is the essence of typical sexual reproduction that gametes are formed in parent individuals by meiosis* and are brought together in fertilization with subsequent formation of a new individual. The process of meiosis, as we shall see, results in a random mixing of the genetic factors and their subsequent random distribution into gametes. Typically, the gametes are formed in separate parents; thus, fertilization results in a set of genetic factors from two different individuals. By this means, the phenomenon of *variability* is made possible in the offspring, and apparently, it provides an advantage that outweighs the disadvantages mentioned above. We shall see later that sexual reproduction and variation have played important roles in the rise of new species, a process which is apparently responsible for the multiplicity of present-day forms.

8.2 The process of meiosis and its significance Inasmuch as sexual reproduction involves the union of gamete nuclei and an accompanying association of the chromosomes which come from each parent, it becomes important to understand certain phenomena that are involved in these processes. Let us suppose that a certain species is characterized by individuals all of whose cells, including gametes, possess ten chromosomes. This means that if gametes of male and female individuals unite, there are twenty chromosomes in the zygote nucleus, and it is not difficult to visualize that unless some mechanism were to reduce the number at one point or another, the chromosomal complement of these organisms would not remain numerically constant.

Fortunately for our understanding of biology, such a mechanism is operative in all organisms that reproduce sexually, except for a few unusual types. It involves a special type of nuclear division called *meiosis* (Gr. *meioun*, to make smaller), accomplished by two successive divisions with the production of four daughter nuclei, each of whose chromosome number is exactly one-half that of the original cell nucleus. Hence, if meiosis occurs in gamete formation, as it does in animals and in a few plants, it results in eggs and sperm whose union merely restores the "double" chromosome number of the species to the zygote, and subsequent mitotic divisions ensure that all cells of the individual possess this characteristic number.

*In most plants, gametes are not formed *directly* by meiosis, as is the case with animals, but the principle is the same in terms of genetic variability.

In order to understand the events which take place in the meiotic process, let us review certain details of ordinary, or mitotic, nuclear division. It will be recalled that prophase is marked by the appearance of distinct chromosomes, each of which is composed of two chromatids connected by a centromere. The chromosomes line up independently of one another along an equatorial plate at metaphase. At anaphase, the centromeres divide, chromatids become separated, and with the subsequent events of telophase and daughter cell formation, each new nucleus comes to possess a representative chromatid of each original chromosome. Thus, if the number of chromosomes appearing at prophase is ten, each new daughter nucleus receives ten chromatids (daughter chromosomes), which duplicate themselves before the onset of new prophases in actively dividing cells (See Section 7.2). Because of this mechanism, chromosome numbers remain constant, and in a quantitative sense, mitotic division is purely *equational*.

As is so often the case with difficult problems in biology, it must be admitted that the forces responsible for initiation of meiotic rather than mitotic division in a given cell are not entirely clear. At any rate, the nucleus of such a cell enters prophase as though it were going to divide mitotically, but the chromosomes behave quite differently than do those in a mitotic nucleus. The descendants of the parental chromosomes, brought together in the zygote that produced the individual and exactly duplicated by many mitoses, now exhibit a strong attraction for each other, and actually unite in a process called *synapsis*. In this union, *homologous* chromosomes (members of a pair) become intimately attached to each other, and because the four chromatids constitute a unit, they are sometimes referred to collectively as a *tetrad* (Figure 8.4). During synapsis, opposing chromatids of homologous chromosomes frequently become coiled and twisted about each other, and they may even exchange portions, an event which has considerable genetic significance. Eventually, there is a meiotic metaphase, and the tetrads line up on a spindle. Characteristically, they separate in the plane of their original union, and the two original chromatids of a chromosome (except for any portions that may have been exchanged with homologous chromatids) move toward one pole in meiotic anaphase, while those of the homologous chromosome move toward the other (Figure 8.4).

With regard to the number of original chromatids, this first meiotic division accomplishes precisely what a mitotic division does, that is, half of the prophase chromatids are delivered to each daughter nucleus. There is a considerable difference, however, in the distribution of these chromatids. In mitosis, one chromatid from each original chromosome becomes situated in a daughter nucleus.

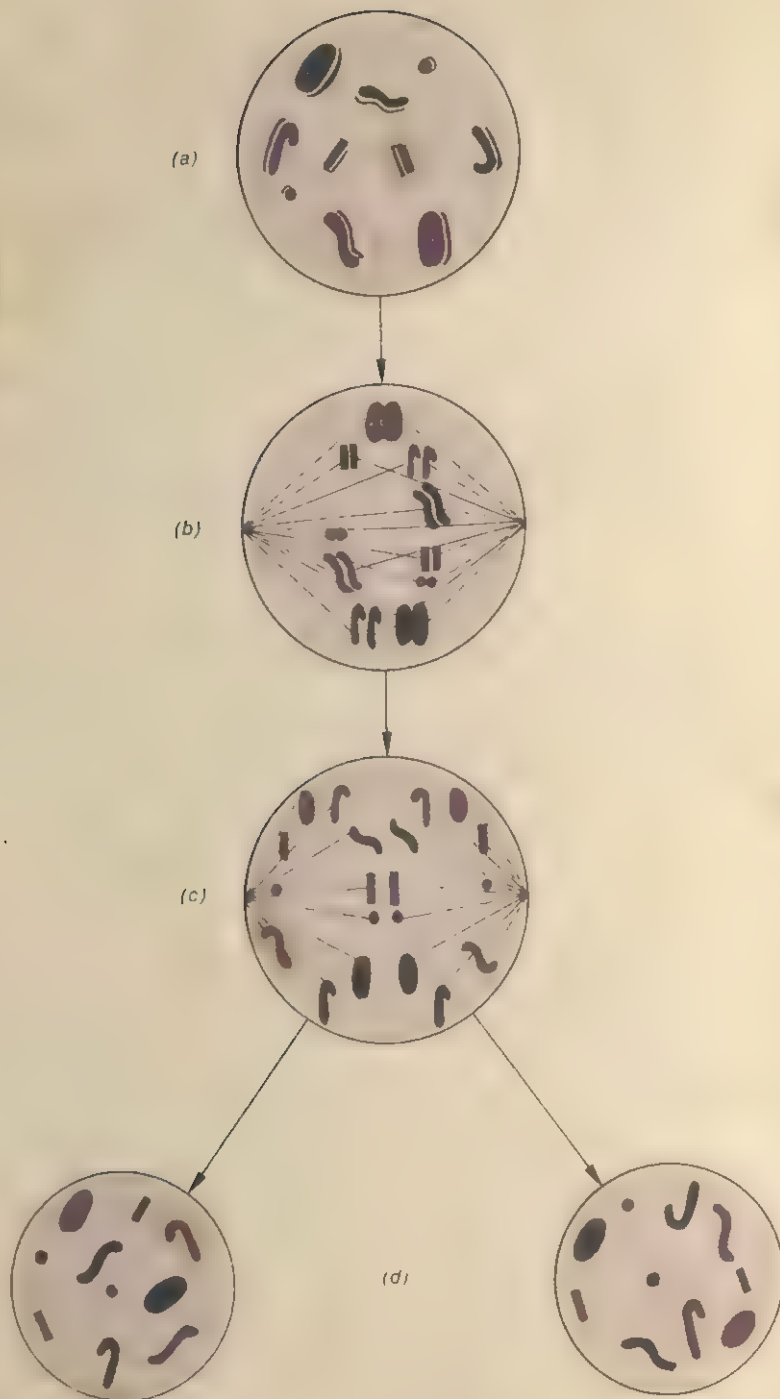
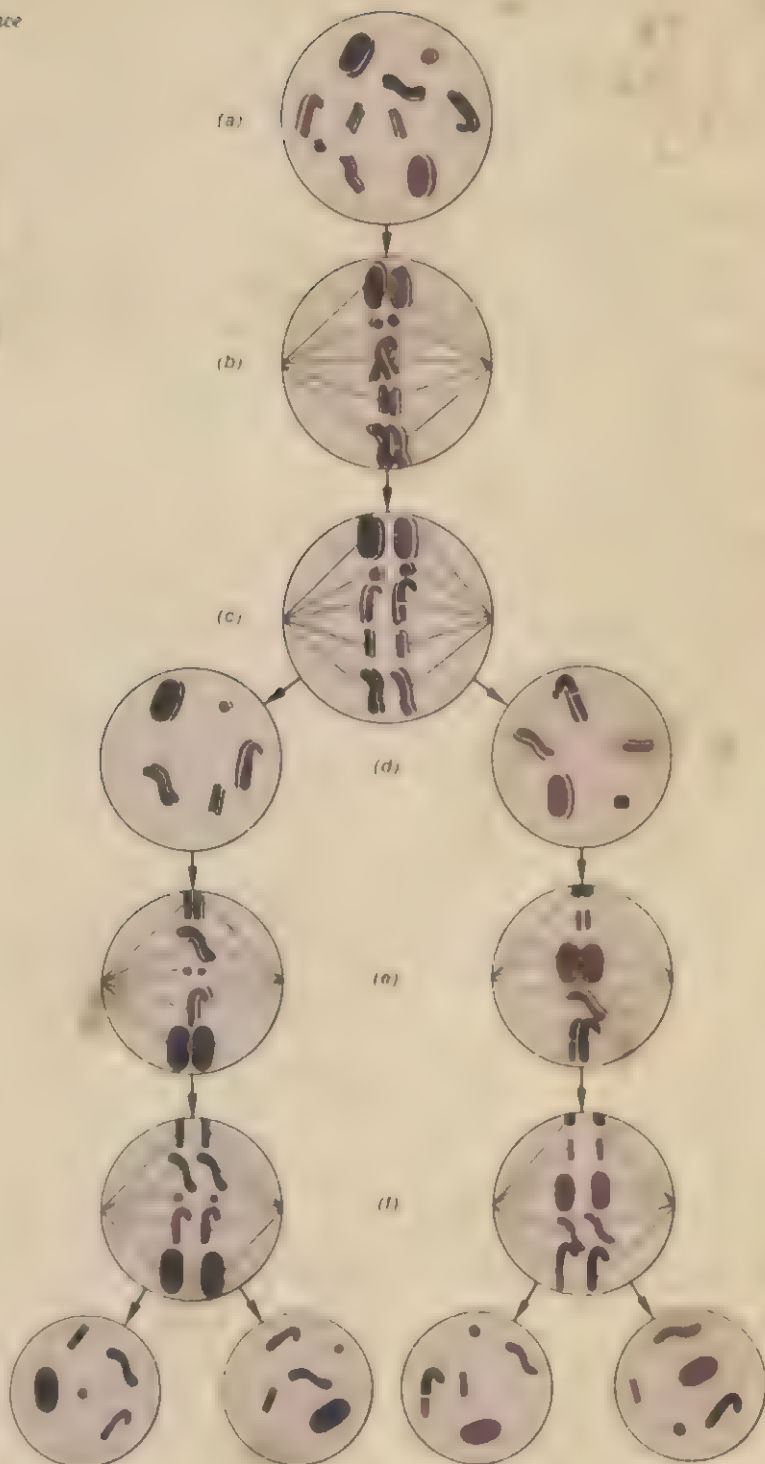


Figure 8.4 Diagrammatic representation of mitosis and meiosis in a hypothetical organism with ten chromosomes. The colored chromosomes came from one parent of the organism, the black chromosomes from the other parent. For the sake of simplicity, only nuclei are illustrated, and nuclear membranes are not shown breaking down. On this page. (a) prophase of mitosis; (b) metaphase; (c) anaphase; (d) end of mitosis. Each daughter nucleus now possesses a representative chromatid of each original chromosome. Compare with Figure 7.1.

Figure 8.4 (cont.) On this page:
meiotic division. In contrast to the figures shown at the left, these are flattened in order to show essential details more clearly. (a) Prophase of nucleus just before synapsis of homologous chromosomes; (b) synapsed chromosomes at metaphase of the first meiotic division, with parental chromosomes oriented randomly. Note that portions of two nonsister chromatids of the J-shaped chromosomes have become crossed upon each other. (c) Anaphase of the first meiotic division; homologous chromosomes separate in the plane of their original union. Note that the above-mentioned portions of two nonsister chromatids of the J-shaped chromosomes have become exchanged. (d) End of first meiotic division; whole chromosomes are located in separate nuclei. (e) Metaphase of second meiotic division; chromatids of each chromosome are preparing to separate. (f) Anaphase of second meiotic division. (g) End of meiosis. Four nuclei now share the twenty original chromatids [see nucleus at (a)]. Note that each nucleus now possesses a chromosome representative of each original chromosome pair.



This is not the case in the first meiotic division: whole chromosomes go into one daughter nucleus, and a second division separates the chromatids. To state the matter differently, a mitotic daughter nucleus receives one chromatid of each *chromosome*, while a meiotic daughter nucleus receives one chromosome (consisting of two chromatids) of each chromosome *pair* characteristic of the species.

Following the separation of chromosomes during the first meiotic division, it would be expected that each nucleus should pass through telophase into interphase. Although nuclear membranes are characteristically formed, the chromosomes tend to retain their individual appearance, and interphase is thus greatly reduced. There is, of course, a great deal of individual variation among organisms and their cells in this respect. In many cells, the chromosomes remain in a prophase-like condition, with their individual identity and form being retained. Regardless of telophase-interphase details following the first meiotic division, each daughter nucleus enters second meiotic metaphase. This time, the chromosomes line up on the spindle in such a way that centromeres divide and sister chromatids separate as in mitosis. Since both daughter nuclei of the original cell undergo this second division, the result is four nuclei, each of which receives a chromatid representing each chromosome *pair* of the original cell. Thus each nucleus resulting from meiotic division has *exactly one-half the number of chromatids* (which may be called chromosomes after they become separated from each other) *as the original cell had chromosomes* (Figure 8.4).

Perhaps the full significance of meiosis will not be apparent immediately since all its implications can hardly be appreciated at once. At least two things should be apparent at this point, however. One of these is that the process of meiosis is *reductional* in terms of chromosome number, resulting in nuclei which possess only one of each original chromosome pair. This is a result of the chromosomes having divided only *once* while the original nucleus divided *twice*. It might be pointed out here that a cell whose nucleus exhibits homologous chromosomes is said to be *diploid* (Gr. *diploos*, double), and one whose nucleus possesses only one member of each chromosome pair is said to be *haploid* (Gr. *haploos*, single). It frequently becomes convenient to refer to the haploid nucleus, cell, or organism by the designation n , while the diploid condition is expressed as $2n$. In the formation of gametes, the reduction of the chromosome number from $2n$ to n eliminates the difficulty which would otherwise exist in maintaining a constant chromosome number for a species. A second significant feature of meiosis is that it provides opportunity for a random mixing of chromosomes in gametes. Whereas each haploid "set" ordinarily must include a representative chromosome

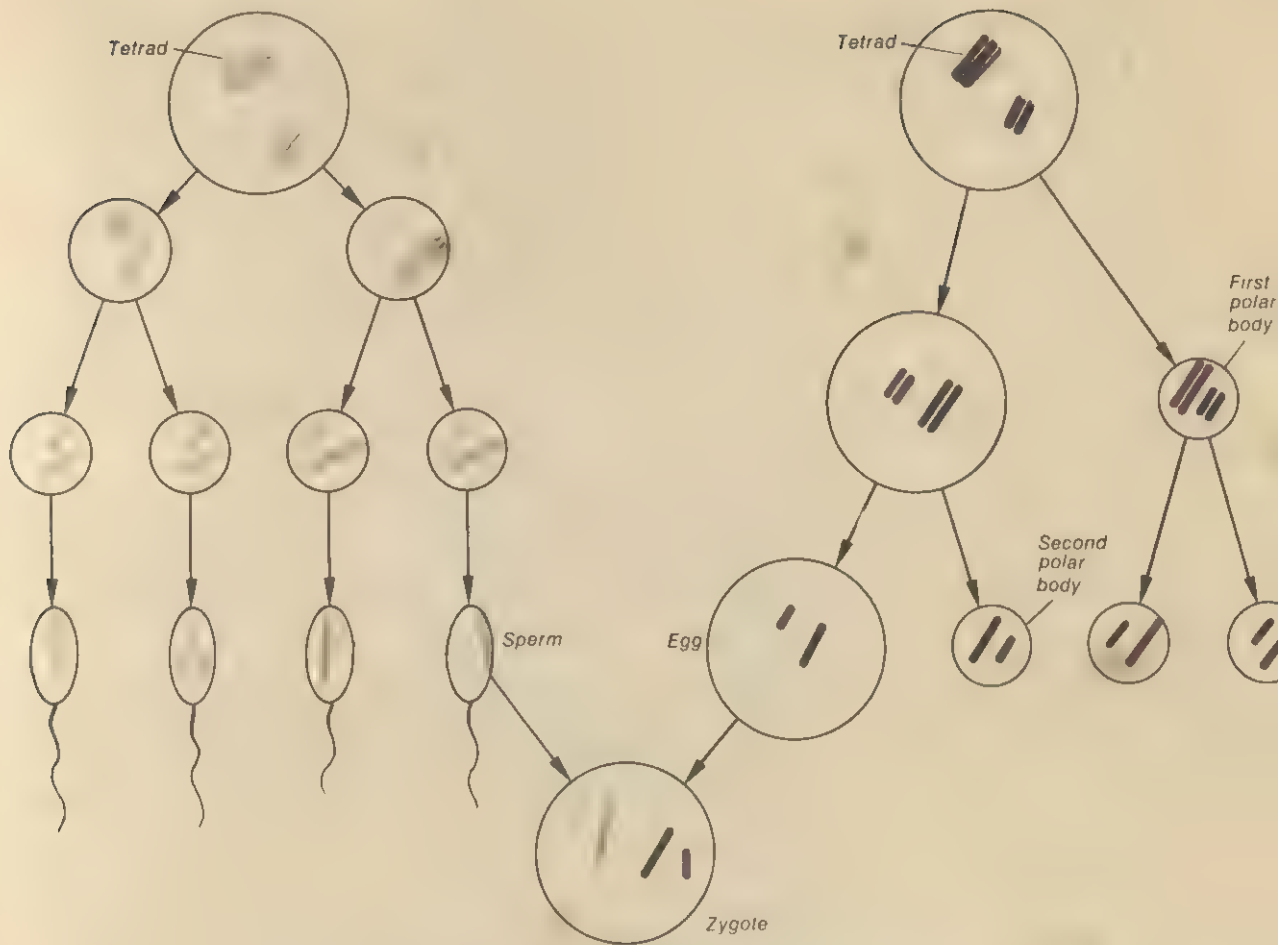


Figure 8.5 A comparison of sperm and egg development in animals. In the interest of simplicity, only two pairs of chromosomes are depicted, and the details of meiosis are omitted

of each homologous pair, the distribution of original parental chromosomes seems to be entirely fortuitous (Figure 8.4). This particular aspect of meiosis and its importance will be developed more fully in a later topic.

Whenever meiosis occurs in the formation of gametes, as described above, it is said to be *gametic*. This is characteristic of animals, where eggs and sperm are normally the only haploid cells in otherwise diploid bodies. It is interesting to note that in typical gamete production in the male animal, the cell which undergoes

meiosis produces four sperm cells, as we would predict, but in the production of eggs, the first meiotic division results in only one functional cell, while the other (called a *polar body*) receives a very small amount of cytoplasm in the divisional process. Although the polar body eventually degenerates and thus plays no further part in the reproductive process, it may undergo the second meiotic division. The functional cell undergoes its final meiotic division with the production of a second polar body, which also degenerates. The net result of this total process, therefore, is the production of only one functional egg instead of the four that would be expected theoretically. This egg, however, has the advantage of possessing all the cytoplasm of the original cell, a feature which makes for considerable biological advantage, since the egg is thus provided with a quantity of food materials which are utilized in embryonic growth following fertilization of the egg (Figure 8.5).

Most plants exhibit *sporic* rather than gametic meiosis, with reduction of chromosome numbers occurring in the production of four haploid spores from a diploid *spore mother cell*. Pollen grains of flowering plants, for example, are such haploid spores (Figure 8.18). In the life cycle of plants whose meiotic process is sporic, there is alternation of a haploid, gamete-producing generation which grows from a spore with a diploid, spore-producing one which arises from a zygote (Figures 8.15, 8.17, 8.20). Although gametic and sporic meiosis are generally characteristic of animals and plants, respectively, certain algae and fungi display a third type, *zygotic* meiosis, where the zygote is the only diploid stage in the life cycle.* Meiosis occurs in such plants during first divisions of the zygote.

8.3 Some examples of sexual reproduction among animals The foregoing portion of this chapter has been devoted to a discussion of terms and concepts that are necessary to an understanding of reproduction as it occurs among organisms. We are now in position to appreciate more fully the actual process as it occurs in representative animal types. A few selected examples will be presented at this point. It should be kept in mind, of course, that there is a great deal of individual variation in the several species of the animal kingdom, and these types which are discussed constitute only a scant survey. In general, however, they may be considered representative.

Paramecium If one obtains a quart or so of water from any pond found in temperate climates and immerses a handful of hay or straw in it, large numbers of *Paramecium* (Figure 4.3) are almost

* It has already been pointed out that certain algae undergo gametic meiosis. Thus, all three types occur in the plant kingdom, with sporic meiosis being by far the most common.

certain to appear in this mixture after it has stood at room temperature for a few days. These protozoa do not arise spontaneously, of course, the hay is a source of nutrient material for a variety of microorganisms already present in the hay, forming a food chain for *Paramecium*, a few of which are present in the pond water. Thus provided with food, they are able to reproduce asexually by division. Microscopic examination reveals that these are relatively large protozoa, capable of rapid motion by virtue of their hair-like cilia. Each individual possesses a large *macronucleus*, which is not directly involved in sexual reproduction, a smaller diploid *micronucleus*, and several other organelles.

Intensive study of this genus has revealed that certain species exhibit multiple sexuality. One variety of *Paramecium bursaria*, for example, has been found to include eight such mating strains (Figure 8.3). As long as one given strain is maintained separately from any other, sexual reproduction does not occur. Upon being mixed with another strain, however, the phenomenon of *conjugation* occurs, in which cells from the two separate strains pair off. The macronucleus of each organism degenerates, and each micronucleus undergoes meiotic division. Four haploid nuclei are formed in the process, three of which degenerate. At this point, definite nuclear material is present in each cell only in the form of one haploid micronucleus. Within each cell, the haploid micronucleus divides mitotically, and one of the two nuclei now seen in each cell moves into the other cell, that is, micronuclei are exchanged. Fusion of the two nuclei now occurs in each of the two cells, and the organisms separate, each possessing a new diploid micronucleus. Subsequent events result in the production of new cells, each with a macronucleus and a micronucleus (Figure 8.6).

Since there is no actual gametic union, and because sexuality is hardly typical, it might seem that conjugation in *Paramecium* does not constitute true sexual reproduction. Although it is obvious that the entire process differs radically from sexual reproduction in more complex animals, the major features of sexuality are exhibited. It is the essence of sexual reproduction that haploid chromosome sets (produced during meiosis) from separate individuals become associated in the production of a zygote nucleus, and this certainly occurs in the conjugation of *Paramecium*.

Hydra The several species belonging to this genus of cnidarians are common inhabitants of freshwater ponds where they may be found attached to submerged leaves or other objects. They are generally less than a half-inch in length, even when the body is elongated to its limit, and it is easy for the inexperienced collector to miss them even when they are present in large numbers. Body struc-

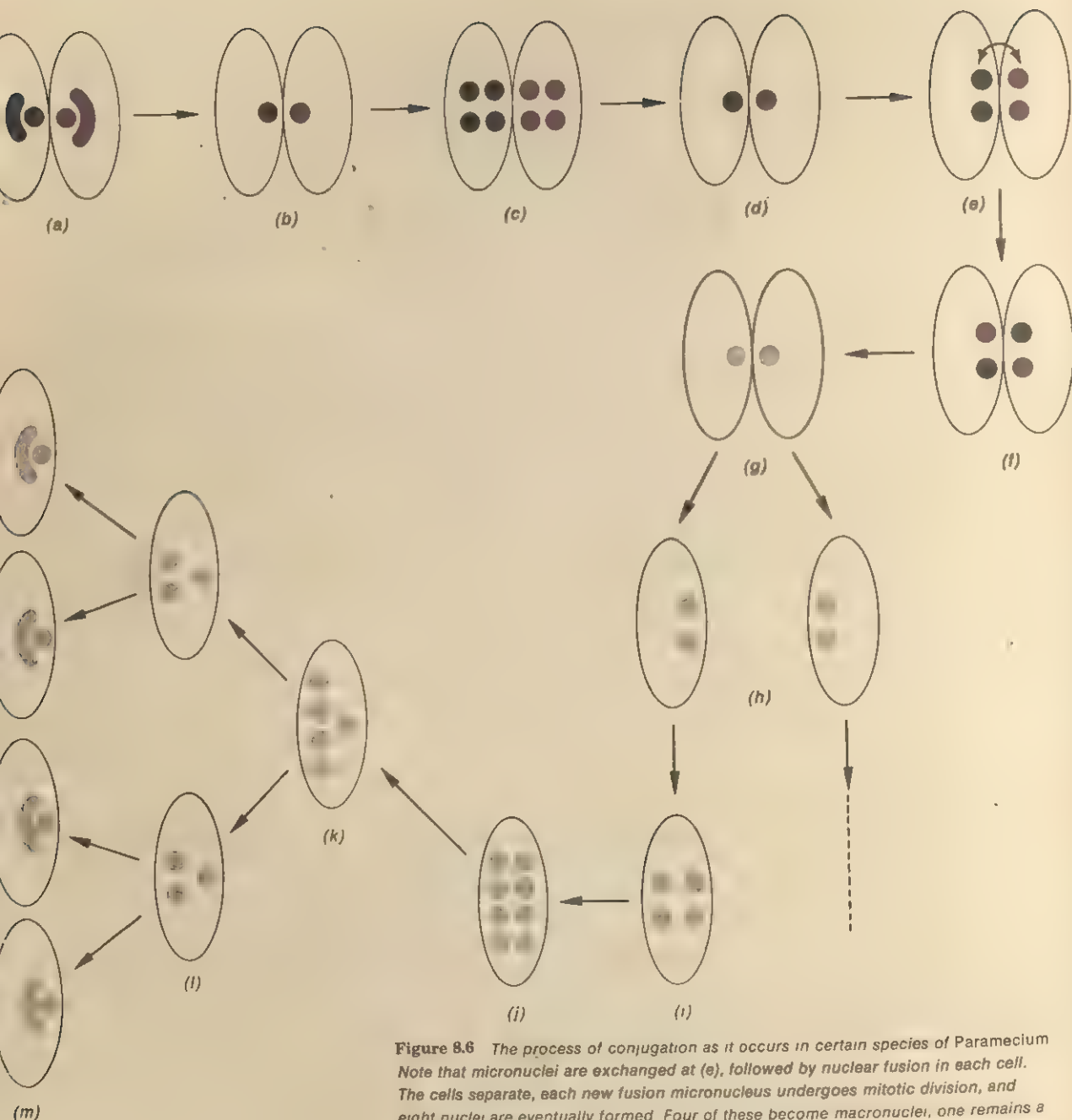


Figure 8.6 The process of conjugation as it occurs in certain species of *Paramecium*. Note that micronuclei are exchanged at (e), followed by nuclear fusion in each cell. The cells separate, each new fusion micronucleus undergoes mitotic division, and eight nuclei are eventually formed. Four of these become macronuclei, one remains a micronucleus, and three disintegrate (k). Two successive divisions of the cell produce four cells occupied by these macronuclei, the micronucleus divides mitotically during these divisions, with the result that four individuals are produced from each original conjugating cell. These may become involved in asexual reproduction indefinitely.

ture is relatively simple, an outer *epidermis* having developed from the embryonic ectoderm, and with endoderm forming the inner *gastrodermis*. There is a network of nerve cells and certain contractile fibers that make limited muscular movement possible. Specialized epidermal cells, concentrated largely on the tentacles, contain bodies called *nematocysts*, each of which releases a coiled thread upon being properly stimulated. These threads carry a paralyzing chemical substance, and they enable *Hydra* to capture smaller animals which are utilized as food. It is enlightening to place a hydra (the generic name may also be used as the common name) in a dish, to guide a smaller animal toward it, and to watch the process of capture. If the victim is taken from the hydra and examined microscopically, it will be seen to have been shot through by some threads and entangled by others. Unless interrupted, the hydra will guide the smaller paralyzed animal into its mouth by using its tentacles, and subsequent digestion occurs within the *gastrovascular cavity*. Structural details of a hydra are shown in Figure 4.5.

We have already mentioned that asexual reproduction may occur in *Hydra* by the process of budding. Sexual reproduction occurs when *testes* (male reproductive organs) or *ovaries* (female reproductive organs) are formed from certain epidermal cells. Some species are *monoecious*, in which case one individual exhibits both types of reproductive organs, while others are *dioecious*, with individuals being definitely males or females. In monoecious species, testes and ovaries generally do not form at the same time, and cross-fertilization thus occurs between different individuals. Several sperm form within a testis, with meiosis occurring in the process, and these eventually escape into the open water. Each is provided with a flagellum, by means of which it swims actively. Meanwhile, a single large egg forms within each ovary of a given animal, meiosis having occurred with the formation of polar bodies. The egg matures and is finally forced out of the ovary, apparently by a splitting of epidermal cells which were greatly stretched by growth of the egg. It remains attached to the surface of the parent animal, however, where it is eventually fertilized by a sperm (Figure 8.7). The haploid sperm and egg unite and form a diploid zygote, and embryogeny of a new individual begins. A blastula is formed, at about which time a thick wall is secreted around the embryo. Gastrulation occurs, the wall becomes thicker, and the embryo drops from the parent body. At this time, it undergoes a period of dormancy, the length of which depends upon several environmental factors. Eventually, the thick wall bursts and development continues with the formation of an adult animal with its specialized cells. It is obvious that further overall development is quite limited from the histological standpoint,

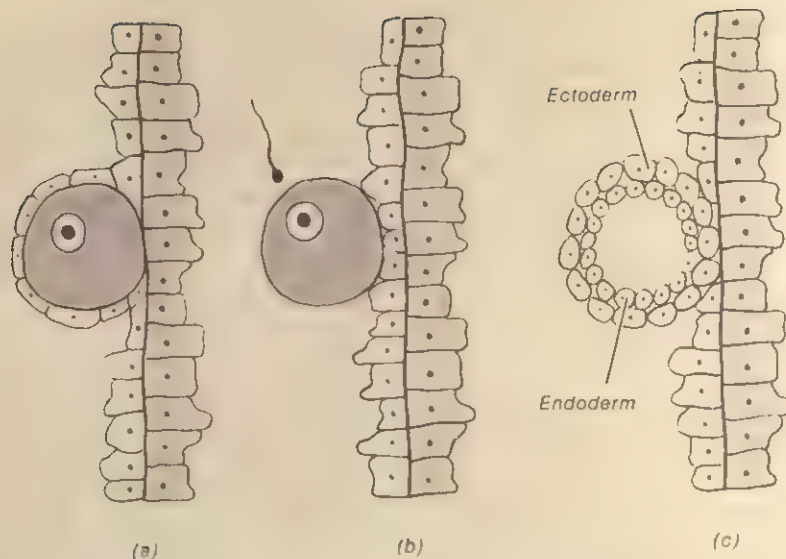


Figure 8.7 Sexual reproduction in Hydra. (a) Egg surrounded by epidermal cells. (b) Egg situated outside epidermis, sperm approaching. (c) Development to gastrula stage, embryo shown in section. It will shortly become separated from the parent animal. The thick wall surrounding the embryo is not shown.

since the fully formed hydra is little more than a gastrula with tentacles (which are merely outpushings of the body proper).

Earthworm Perhaps few animals are more widely known and easily recognized than is the earthworm, *Lumbricus terrestris*, a member of the phylum Annelida. A study of its over-all morphology reveals the presence of advanced structural organization, including well-developed nervous, muscular, and circulatory systems. In its life habits, the earthworm spends most of the time beneath the surface of the soil, where it forms burrows and tunnels by actually eating its way along, although if the soil is quite soft, it may simply push its way through. The ingestion of soil serves a twofold function; the worm is able to construct an elaborate system of tunnels, eventually depositing the castings on the surface of the soil, and it derives nutritive benefit from such organic materials as are digestible in the gastro-intestinal tract. For both of these reasons, the earthworm is of positive economic importance to the farmer. Air may penetrate the soil to greater depths by virtue of the tunnels, thus hastening decomposition of organic materials by aerobic microorganisms, and the digestive and metabolic activities of the earthworm contribute to soil fertility. It has been shown that greater crop yields are obtained from soil containing earthworms than from similar soil which is devoid of them.

As is characteristic of all but the lowest animals in the phylogenetic scale, the earthworm does not reproduce asexually. In its sexual reproduction, each individual possesses functional ovaries and testes (in which meiotic divisions produce haploid eggs and

sperm) and is thus hermaphroditic. Self-fertilization does not occur, nor is any mechanism operative whereby sperm may travel freely from one individual to another, as is the case with *Hydra*, whose habitat is aquatic rather than terrestrial. Instead, two earthworms establish body contact in the act of *copulation*, or sexual union, during which the two individuals exchange sperm (Figure 8.8). These are received by special receptacles in each worm where they are retained for a time. Eventually, eggs are formed in ovaries which lie behind the sperm receptacles and in front of the *clitellum*, an obvious band which encircles the worm beginning at the thirty-first or thirty-second segment from the anterior end. At about the time of egg formation, the clitellum secretes a thick layer of mucous which gradually slips forward. As it passes the oviduct openings (located on the fourteenth segment), this mucous layer receives a number of eggs. Similarly, sperm are received at the openings of the receptacles (segments 9 through 11), and fertilization occurs. As the mucous layer finally slips off the anterior end and is deposited in the soil, its elasticity causes it to close, forming a pear-shaped *cocoon* whose greatest diameter is approximately that of a printed capital O. There is a period of egg production by the worm, during which several cocoons may be produced in a similar manner. It has been reported that only one fertilized egg develops within each cocoon, even though several are present. Blastulation, gastrulation, germ layer formation, and further specialized embryogeny occur, and the young worm thus formed eventually breaks through the cocoon and begins an independent existence.

The honeybee Most insects, including the honeybee (*Apis mellifera*), exhibit a life cycle in which more than one form of body structure is seen. Because bees are *social* insects, forming large



Figure 8.8 Earthworms in copulation.
(General Biological Supply House, Inc.)

hives wherein a complex division of labor and a high degree of organization are developed, they are not to be considered typical either in this respect or in their reproductive habits, but several interesting features regarding the latter are worthy of our attention at this point (Figure 8.9).

Ordinarily, only one reproducing female bee, the queen, is present in a hive. From a single mating early in her life, she receives a supply of sperm which she may retain in a viable state over a period of years. As she produces fertilized eggs, which she is able to lay in prodigious numbers, they are placed in special wax cells of the hive by worker bees. In about three days these eggs develop into *larvae*, which are small, wormlike forms that bear little resemblance to adult bees. Among the nonsocial insects, the larval form is generally free living (for example, the "caterpillar" of the butterfly life cycle), but honeybee larvae remain within their wax cells, which are not completely closed. They are fed by "nurse" workers for about five days, during which time they grow tremendously. Following this period, the larva spins a cocoon, and for about fifteen days it exists as a *pupa*, in which stage it undergoes drastic body changes. Finally, the adult bee emerges from the cocoon and chews its way out of the cell. It is now ready to take its place in the hive as a worker bee.

Individuals produced in the manner described above are all sterile females, incapable of reproduction, and it is obvious that unless functional males and females are present at some point, the species could not persist. It has been found that fertilized eggs laid by the queen will develop into functional females (queens) if they are fed a special diet called "royal jelly" during the entire larval period. This is apparently done when the hive has become sufficiently large to divide. At this time, a dozen or so larvae are given the special diet, and following their pupation (which requires only some eleven days, as compared with fifteen for workers) they emerge from their cells. If one queen hatches well ahead of the others, she may locate the remaining queen pupae and sting them to death in their cells, or if all emerge within a short time of each other, a fight to the death occurs. At any rate, only one queen survives.

At a time previous to the development of queens, a number of functional males, called *drones*, were produced from unfertilized eggs. In other words, unfertilized eggs actually develop into adult individuals by a process called parthenogenesis (see Section 8.5). The drones apparently serve no useful function in the society until the surviving new queen emerges from the hive for her "nuptial flight." At this point, she flies high into the air, and the drones follow her. The strongest of these is able to overtake and mate with her, while the others either die from exhaustion or return to the hive.



Figure 8.9 Left to right: worker, queen, and drone bees. (U.S. Department of Agriculture.)

where they are immediately stung to death by workers. (The successful drone actually enjoys little advantage over the others, since the act of copulation proves fatal to him through the loss of reproductive organs and body parts to which they are attached.) The queen returns to the hive, and either she or the old queen leaves to establish a new colony. The workers divide themselves between the two queens, and a "swarm" is formed by the departing group. Actually, there are several possible variations of timing with regard to the production of new queens and the division of the hive. The account given above is a very general one.

Some interesting cytological factors are operative in the reproductive process of the honeybee. Cells of queens and workers are diploid, and meiosis occurs in egg production according to normal procedure. Fertilization of the haploid egg by a haploid sperm results in a diploid individual, as is the usual case in animal reproduction. Because the drone develops from a haploid cell, however, its body cells are haploid, and sperm production is not accompanied by meiosis. Although the honeybee is not the only animal to exhibit such a reproductive cycle, it is quite unusual for a sexually reproducing animal not to undergo meiosis in the production of gametes.

Because insects constitute a large and varied class of the phylum Arthropoda, with many details of reproduction differing from group to group, the honeybee should not be considered typical in this characteristic. For one thing, it is a social species, which is not true

of the vast majority of insects, and the life cycle with its various accompaniments is obviously a reflection of this mode of existence. In its cycle of egg-larva-pupa-adult, however, it resembles most insects. Certain orders, such as that including grasshoppers, are not characterized by the development of these body forms (called *complete metamorphosis*); rather, the egg hatches into a form which resembles the adult either very closely or to a considerable degree (*incomplete metamorphosis*). Changes which occur with growth to the adult stage, therefore, are much less dramatic than in forms which undergo complete metamorphosis.

The frog Inasmuch as all species of frogs reproduce in essentially the same manner, the following description may be considered valid for the group. Like practically all vertebrates and most higher invertebrates, frogs are definitely either males or females, that is, species are dioecious. The mating season occurs in the spring, at which time eggs and sperm develop in mature individuals. In the mating process, the male frog clasps the female and may remain astride her back for several days. Eventually, her eggs are released into water from the vent,* at which time the male discharges sperm upon them. The eggs are thus fertilized in the water, where they undergo development, and the male releases the female. True copulation, which involves the introduction of sperm from one animal into another, does not occur here; the act of sexual union in frogs is sometimes called pseudocopulation, and fertilization is external to the body of the female. It is interesting to note that copulation is not characteristic of the fishes, whereas it is of the land-dwelling vertebrates and aquatic mammals; thus frogs, which are amphibians, are in an intermediate position. This is only one of a great many structural and behavioral characteristics of amphibians that are intermediate between the two groups.

After fertilization, frog eggs undergo cleavage and eventually pass through blastula and gastrula stages. Further specialized development occurs, resulting in the formation of a *tadpole* within a few days after fertilization. The tadpole is equipped with gills which enable oxygen to diffuse from the water into the blood stream, and it remains aquatic for a period which varies considerably among frog species. Gradually, metamorphosis results in the growth of limbs, loss of the tail, disappearance of gills and appearance of lungs, plus a great many less obvious changes (Figure 8.10). Thus, the frog is

*Technically, the posterior opening of the frog is not an anus. Most vertebrates except mammals exhibit a common collecting reservoir, the *cloaca*, into which fecal, urinary and genital products are emptied. Since an anus is the posterior opening of a gastro-intestinal tract, the term *vent* is accurate in describing the posterior cloacal opening.

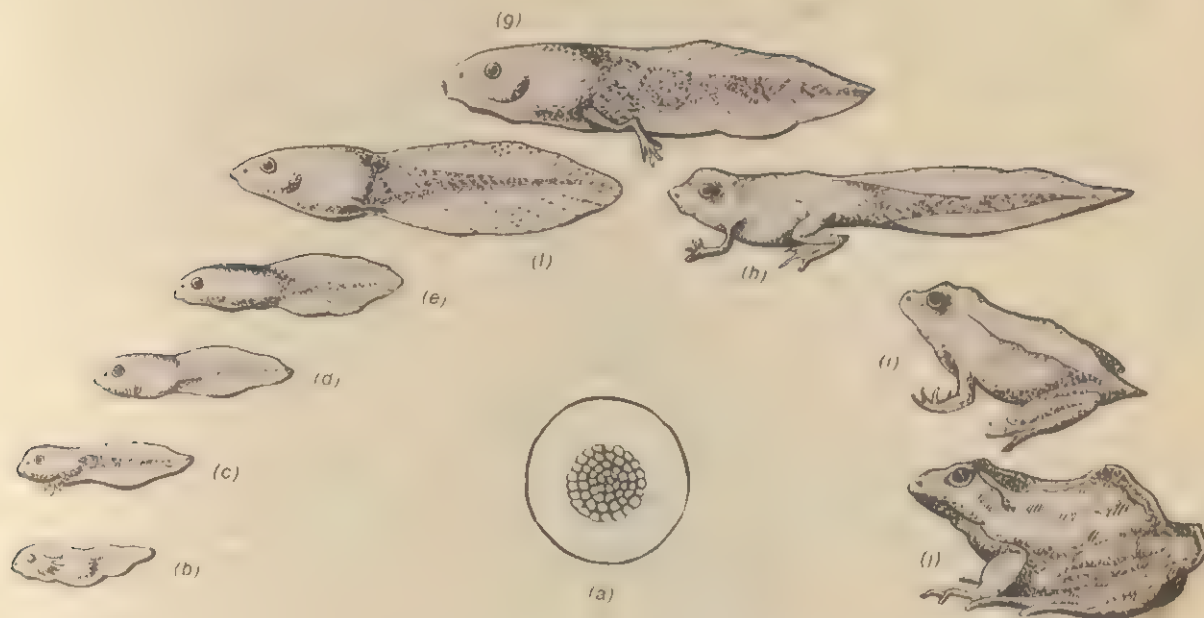


Figure 8.10 Development of the frog. (a) Embryo at blastula stage, surface view, surrounded by original gelatinous material of egg (b) Young embryo equipped with gills. (c–h) Further development. Note the appearance of legs and the disappearance of gills. (i) Tail becomes very short; individual spends most of its time on land. (j) Fully developed frog.

aquatic in its early life and terrestrial at maturity. When testes and ovaries become functional in male and female frogs, respectively, meiosis results in the production of haploid reproductive cells. Union of sperm and egg, of course, restores the diploid condition characteristic of cells other than gametes.

The human As an example of reproduction in the most highly developed animals, the mammals, we shall consider the process as it occurs in the human species. Selection of the human as a representative mammal should not convey the idea that reproduction in man is ideally typical of the class to which he belongs; it is felt that an account of sexual reproduction in selected animal types would hardly be complete without some mention of our own species, and important deviations from more typical mammalian reproduction will be pointed out (Figure 8.11).

Although seasonal reproductive periods have been and still are important among certain primitive human groups, as is the case with various other mammals, civilized peoples of the present day are not so restricted. Sex drive remains fairly constant in a given human

without regard to seasons or sexual cycles.* There is a restriction, however, on the time that a pregnancy can be established in the female. The human is one of a relatively small group of mammals (specifically, certain of the primates) the females of which exhibit a *menstrual cycle*, marked by a periodic build-up of tissue in an organ called the *uterus*, followed eventually by dissolution of this tissue and its passage to the outside of the body unless the cycle is interrupted by egg fertilization. In the human female, this cycle begins at *puberty* (the beginning of sexual maturity), which normally occurs at about twelve to fourteen years of age, and continues until *menopause* (the end of the reproductive span) some thirty or more years later. It repeats itself approximately every twenty-eight days, with an egg being released (*ovulation*) from one of the two ovaries at some time during each period. If the beginning of menstrual flow is counted as the first day of a cycle, ovulation generally occurs in fourteen plus or minus five days, although there may be exceptions to this pattern. Upon being released from the ovary, an egg enters the open end of a *fallopian tube* and is conveyed toward the uterus. If sperm have been introduced into the vagina and travel upward through the uterus and fallopian tubes, one of them may fertilize the egg if a sufficient number reach it while the egg is in about the upper one-third of the tube.† Thus, a pregnancy can be established only during a brief period following ovulation, the duration of which may be only twenty-four hours or less. At no other time during the cycle can fertilization occur.

In the event that the egg is fertilized, it continues to move toward the uterus, where it becomes imbedded within about ten days. Meanwhile, the zygote has undergone cleavage, and embryonic development is well under way by the time it reaches the uterus, the lining of which is kept intact by hormonal controls initiated by the embryo itself. Also by this time, the food material of the original egg has been exhausted by the embryo in its developmental activities, and it establishes a nutritive relationship with the lining of the uterus. At first, food materials and oxygen diffuse into the embryo from the surrounding uterine tissue, and waste materials pass outward. However, a special organ called the *placenta* is established between

* In a number of mammals, the female experiences sex urge only when eggs are released from the ovaries, a process which is under the control of hormones (internal glandular secretions), and which occurs at a certain time in a regulated cycle. In such species, of which most domesticated mammals are typical, the female will receive the male (whose sex drive remains constant) at no other time.

† The human egg (Figure 8.1) is surrounded by a thick layer of material which cannot be penetrated by a single sperm. However, each sperm carries a small amount of an enzyme that is capable of digesting away this material, and after several thousand have contributed to this effect, one penetrates the cell membrane and fertilizes the egg.

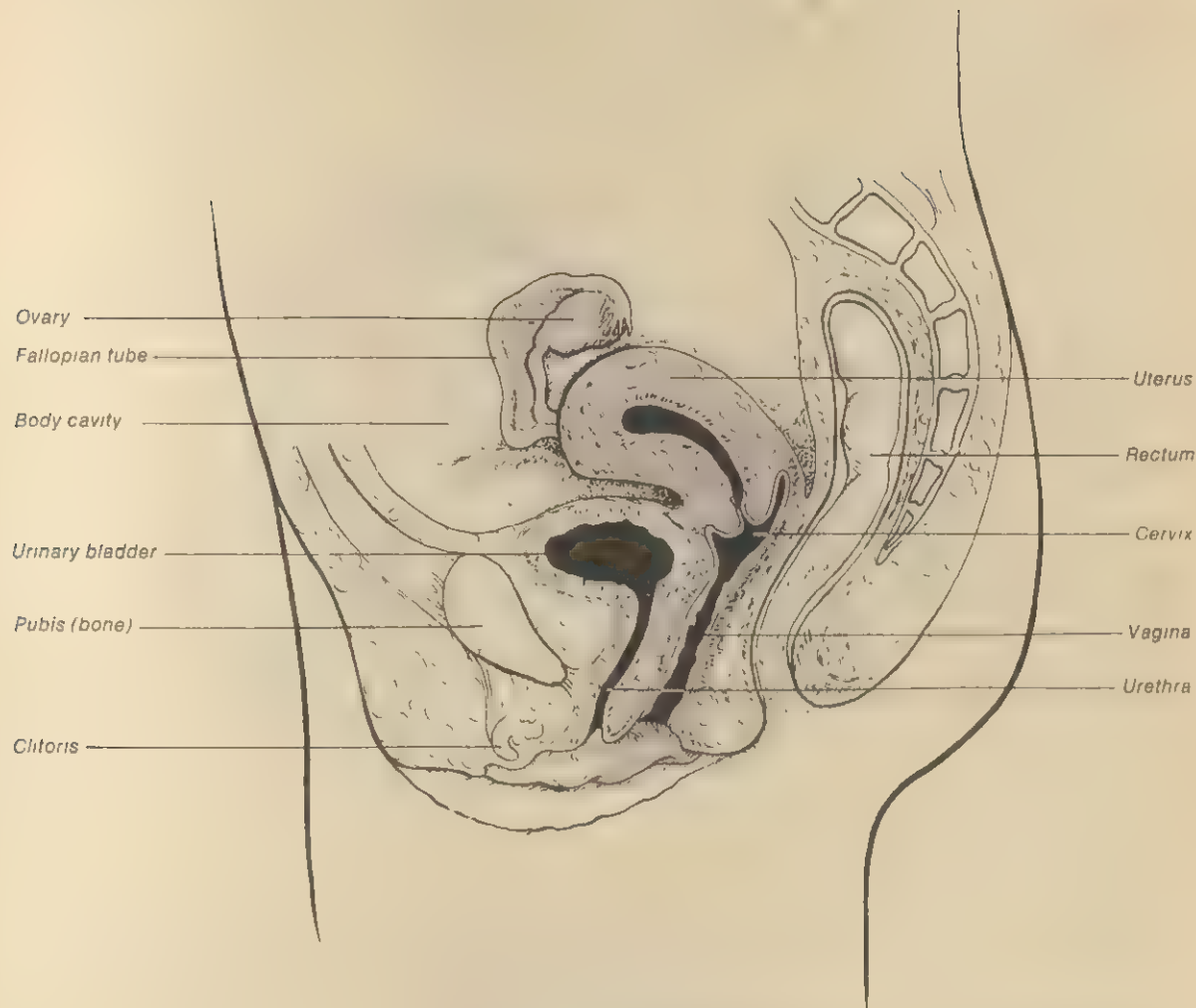


Figure 8.11 Human female reproductive system, as seen in a midsagittal section through the pelvic region.

mother and embryo rather early in development, and it functions in the exchange of materials.

For several weeks, development proceeds with the formation of primary germ layers and subsequent growth of body organs. A heart and circulatory system appear rather early, and blood circulation begins. It should be pointed out that there is normally no actual mixing of maternal and embryonic blood, although they are brought into close proximity in the placenta.

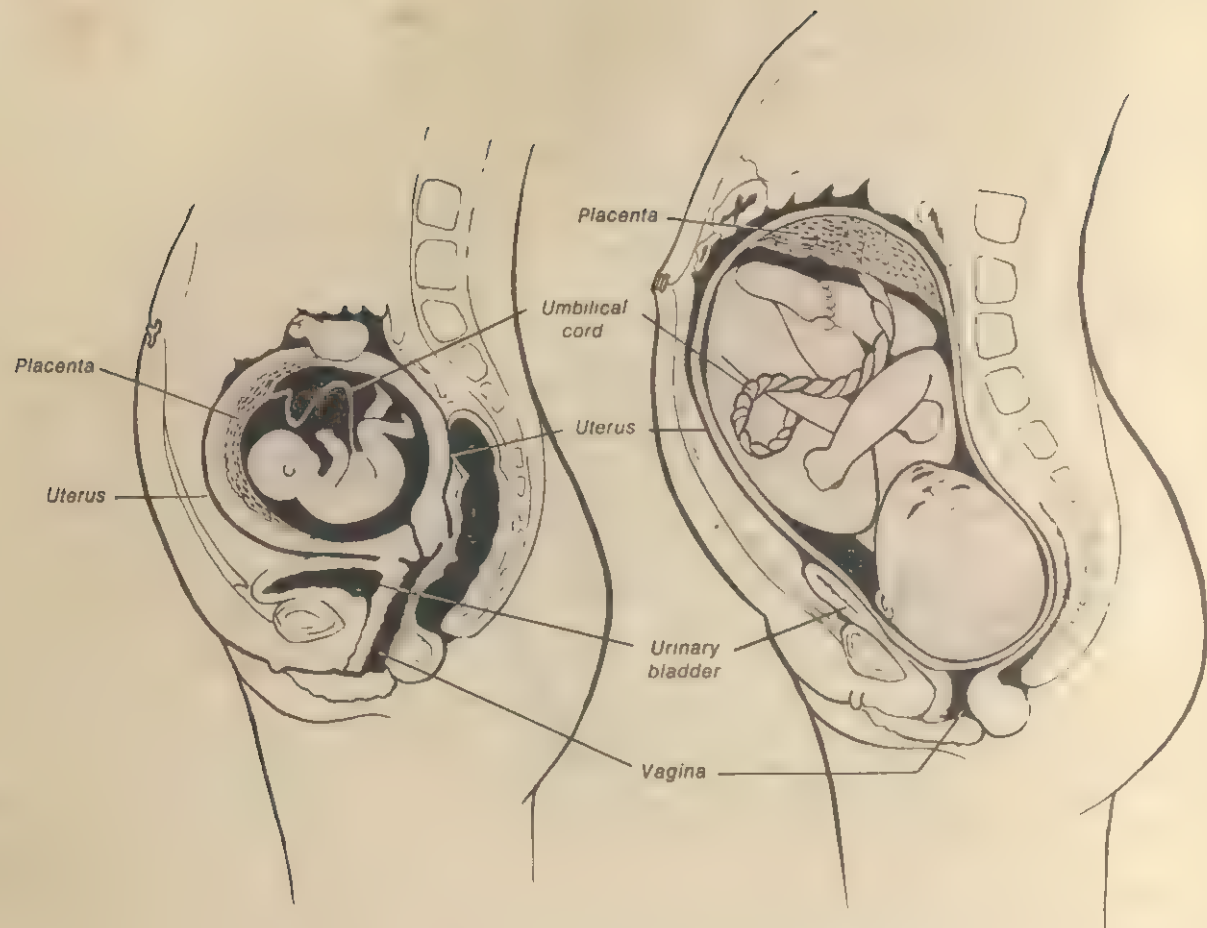


Figure 8.12 Human female reproductive system during pregnancy. (a) Fetus at about four months of development; (b) fetus at full term. The developing individual is contained within a fluid-filled sac inside the uterus and is connected to the placenta by means of the umbilical cord.

During the first several weeks, the developing individual hardly resembles a human being. In fact, stages are experienced during which pharyngeal pouches and a tail are evident, to mention only two of the many features which human embryos share in common with those of other vertebrates. At the end of about three months, however, it begins to resemble a post-natal human, and it is now termed a *fetus* instead of an embryo. (Figure 8.12). Since most specialized development has already occurred at this stage, the remainder of time spent by the fetus inside the uterus is largely devoted to

growth. After some nine calendar months of total development, a complex series of hormonal effects result in contraction of the uterus, and the fully formed infant is expelled. Following a period of adjustment on the part of her reproductive system, the mother experiences resumption of the menstrual cycle. In the new individual thus formed, reproductive organs appear during embryonic development, and these remain generally inactive until puberty. At this time, mitotic and meiotic divisions are initiated among the *primordial germ cells*, and haploid gametes are formed.

In a number of mammals (for example, the pig) more than one egg is discharged during ovulation, with the result that several offspring may develop at one time within the uterus. In such animals, each embryo forms a separate placenta. In the human and other mammals which normally produce only one offspring at a time, multiple births are not at all rare. When they occur, one of two things must happen. Either the ovaries release more than one egg at a



Figure 8.13 Generalized animal life cycle. Dotted line indicates point in the cycle at which meiosis occurs.

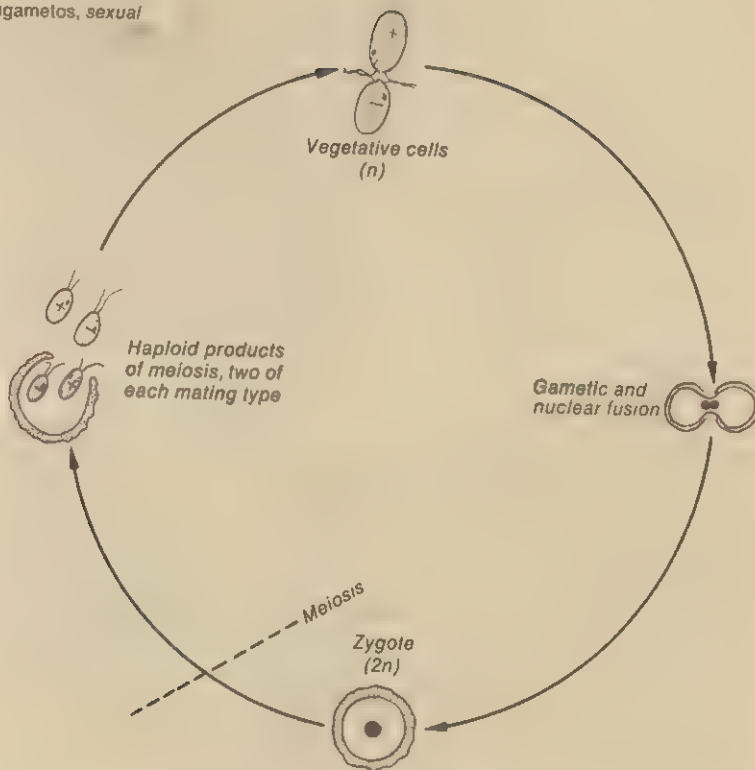
given ovulation, in which case human offspring do not resemble each other to any greater extent than do ordinary brothers and sisters, or abnormal division of the embryo during early development results in two or more embryos, with the result that offspring are genetically identical. Whenever this occurs, it provides an interesting and significant example of reproduction which is both sexual and asexual. The union of sperm and egg in the formation of the zygote is, of course, sexual reproduction. However, a subsequent division of this zygote or of an early embryo is entirely asexual, as indicated by the identical duplication of genetic factors. Whenever identical twins appear in a human population, for example, it provides a dramatic example of the difference in sexual and asexual reproduction as regards genetic variability. At any level, even in human reproduction, asexual reproduction provides no opportunity for a random mixing of genetic factors, as does sexual reproduction. In the final analysis, this is probably the most significant difference between these two modes of reproduction.

8.4 Some examples of sexual reproduction among plants There is a tendency on the part of most people to regard sexual reproduction as being restricted to the animal kingdom, chiefly because the process occurs in plants in a far less obvious manner than in most animals, and it thus requires closer study in order to observe and to understand it. The plants discussed below are fairly representative of the plant kingdom as a whole with respect to sexual reproduction, and they will serve to demonstrate that most plants, like the vast majority of animals, do exhibit sexuality.

Chlamydomonas This organism is one of a large number of green algae which are widespread in soil and fresh water. A great many species have been described as belonging to this genus; the description given below is generally valid for all members, but it applies specifically to *Chlamydomonas eugametos*, which has been one of the most widely studied species of the group. Individuals are unicellular, and each possesses a single *nucleus*, *chloroplast*, *eyespot*, and *pyrenoid*, the last-named organelle serving as a center of starch accumulation during photosynthesis. There are two (or sometimes more) contractile vacuoles at one end of the cell which function in osmotic regulation, and two whip-like *flagella* make it possible for the cell to achieve motility (Figure 7.2a).

A given cell of *Chlamydomonas*, under ideal conditions, grows in size and undergoes mitotic nuclear division accompanied by cytokinesis, a process which repeats itself with each new cell thus produced. Therefore, continued cell division, as we learned to be the case in *Paramecium*, is equivalent to asexual reproduction. It was

Figure 8.14 Life cycle of *Chlamydomonas eugametos*, sexual phase



pointed out earlier that cytokinesis in *Chlamydomonas* is somewhat different from that occurring in either typical plant or animal cell division.

Sexuality has been studied quite extensively in a number of species belonging to this genus, and it has been found that in *C. eugametos* and certain other species two strains exist which are morphologically indistinguishable with regard to sex. When these are mixed under proper conditions, there is an attraction between cells of the two strains, and these eventually pair off, with subsequent protoplasmic and nuclear fusion. Thus, the organisms (cells) themselves function as gametes, and a zygote is formed. It has been found that the zygote undergoes two successive meiotic divisions with the production of four individuals, which escape from the old zygote wall.* Hence, meiosis is zygotic, and the zygote is the only diploid structure in the cycle (Figure 8.14).

* In some species (including *C. eugametos*), the four products of meiosis may divide mitotically within the zygote wall and form more cells before escape is effected.

In its exhibition of zygotic meiosis and morphologically indistinguishable sexual strains, *C. eugametos* is typical of a great many algae and fungi. *Rhizopus stolonifer*, the bread mold (Figures 4.29, 8.2), is one fungus of which this is true. Thus, sexuality in these "lower" plants is somewhat different from that observed in the more complex plants and animals, but it meets all the requirements of our previous definition.

Mosses Although most people are vaguely familiar with the group of plants called mosses, it is doubtful that many students beginning a formal study of biology know very much about them. These plants are widespread in nature, occurring most abundantly in moist, shaded areas where they may cover the ground with a carpet-

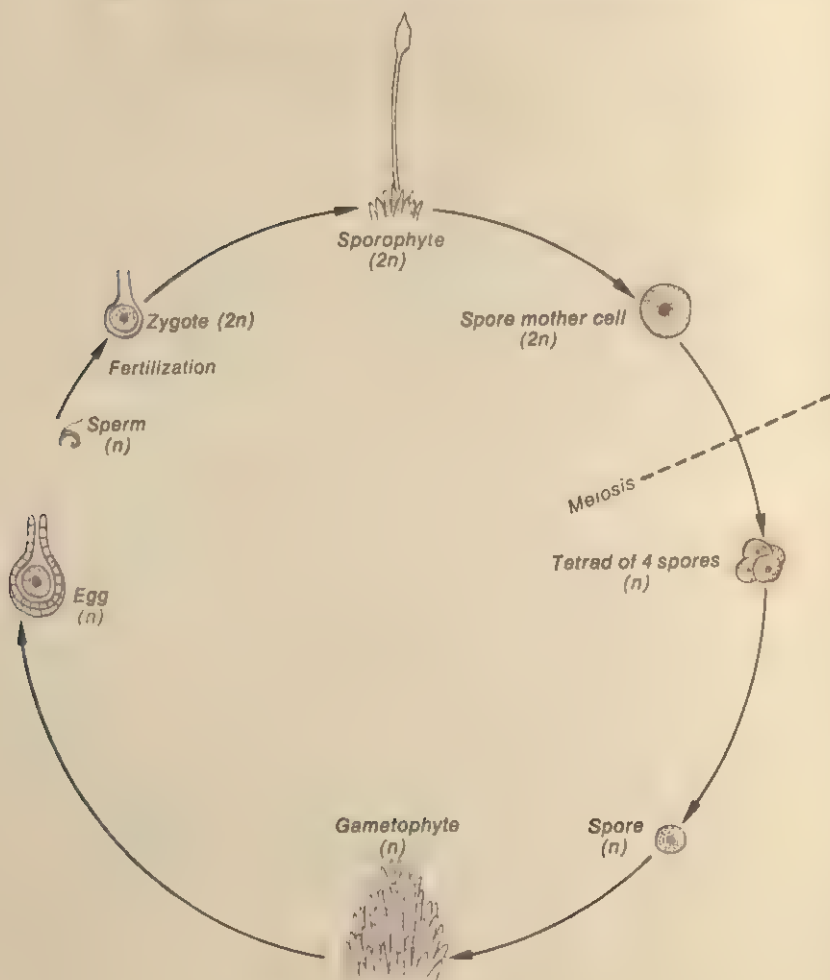


Figure 8.15 Life cycle of a moss

like growth. Close examination of a typical mossy area leads to the observation that many small, leafy plants make up the growth and that at certain seasons some of these plants may bear an elongated structure which resembles, more or less, a golf club.

The green, leafy plants are actually gamete-producing individuals (gametophytes), and in many species of mosses they are definitely either males or females. In others, one plant may produce both eggs and sperm, in which case there may appear male and female branches, or both types of sex organs may occur on the same branch. At any rate, sperm escape from the organ within which they are formed at a time when there is adequate moisture for them to achieve motility, and they reach female plants (or branches) and fertilize eggs, which develop individually within vase-like structures. Several eggs in the same plant may be fertilized, but only one zygote develops fully at the tip of a given female plant or branch. Repeated cell division results in the formation of the elongated structure referred to above, which bears a sporangium, or spore-producing organ, at its terminal end (Figure 4.31). For this reason, the product of zygote development is called a sporophyte.

Botanists have learned that the gametophytes develop from spores produced in the sporangium and that both spores and the cells of these plants, including their gametes, are haploid. The sporophyte develops from a diploid zygote, and it is thus composed of diploid cells. Meiosis occurs in *spore mother cells* of the sporangium and four haploid spores are thus produced from each. Hence meiosis is *sporic*, as is typical of plants (Figure 8.15).

Botanists regard the moss gametophyte and sporophyte of a given species as two distinct phases of a life cycle, since one is haploid in chromosomal constitution and produces gametes, and the other is diploid and spore-producing. Thus, the moss is said to exhibit *alternation of generations*. Since the gametophyte is the more prominent and persistent generation in mosses, it is said to be the *dominant phase of the life cycle in this group*.

Ferns It was pointed out in an earlier chapter that land plants characterized by vascular tissue may attain greater size than those without it, as a general rule, since they are able to conduct water and dissolved minerals to greater heights. In contrasting a typical fern with even the largest of the mosses, the difference in body size is immediately apparent. In addition to this difference, ferns demonstrate a considerable advance in complexity over mosses, exhibiting highly developed stems and roots, both of which typically grow beneath the soil surface, and leaves, which make up the visible part of the fern. The leaves are usually quite large, and at certain times they may bear sporangia (Figure 8.16b) on their lower surfaces. The

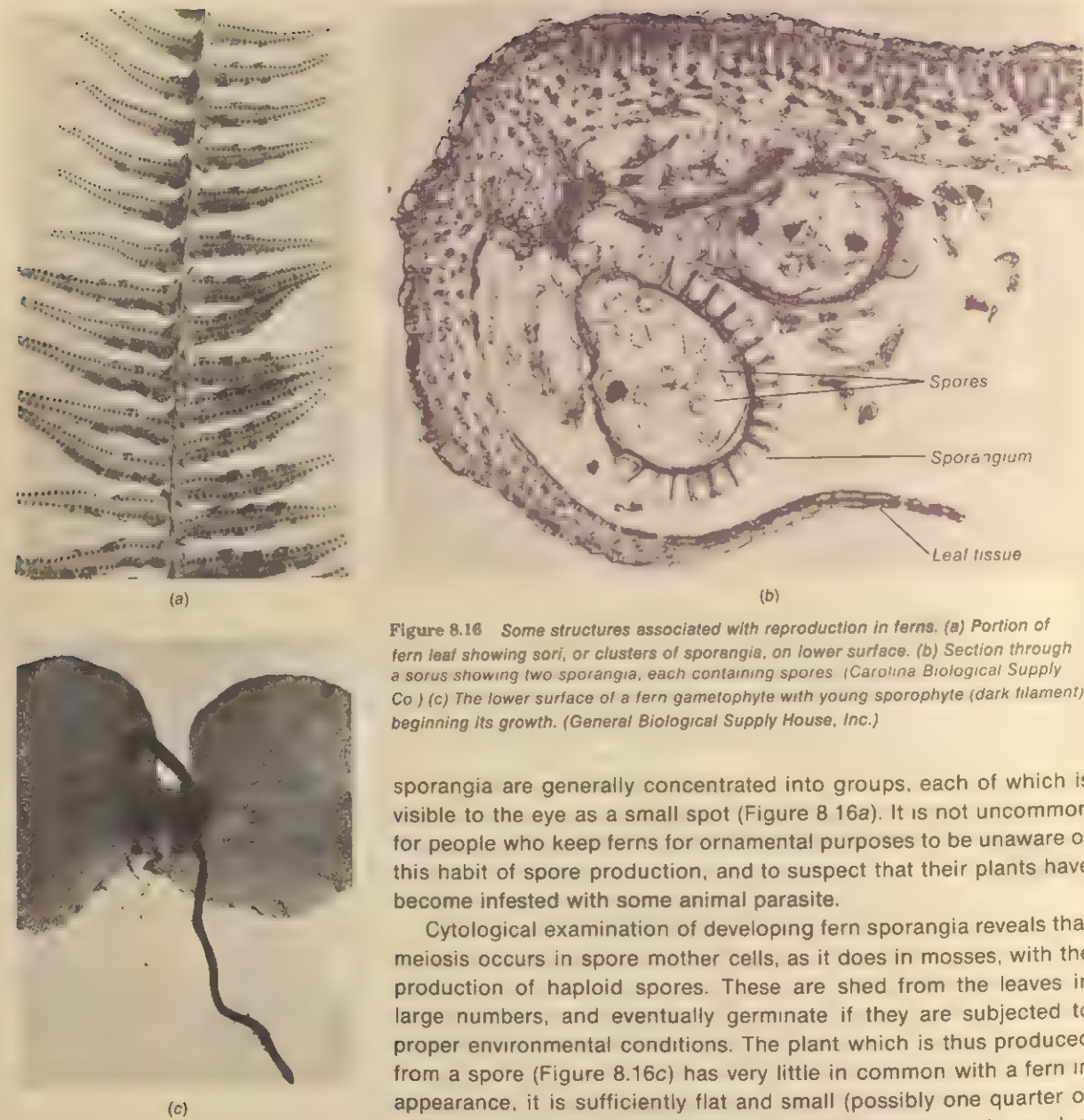


Figure 8.16 Some structures associated with reproduction in ferns. (a) Portion of fern leaf showing sori, or clusters of sporangia, on lower surface. (b) Section through a sorus showing two sporangia, each containing spores (Carolina Biological Supply Co.) (c) The lower surface of a fern gametophyte with young sporophyte (dark filament) beginning its growth. (General Biological Supply House, Inc.)

sporangia are generally concentrated into groups, each of which is visible to the eye as a small spot (Figure 8.16a). It is not uncommon for people who keep ferns for ornamental purposes to be unaware of this habit of spore production, and to suspect that their plants have become infested with some animal parasite.

Cytological examination of developing fern sporangia reveals that meiosis occurs in spore mother cells, as it does in mosses, with the production of haploid spores. These are shed from the leaves in large numbers, and eventually germinate if they are subjected to proper environmental conditions. The plant which is thus produced from a spore (Figure 8.16c) has very little in common with a fern in appearance, it is sufficiently flat and small (possibly one quarter of an inch in diameter in many ferns) as to escape detection by any but the practiced eye. This is the gametophytic stage of a cycle which is essentially similar to that of a moss, and it functions in the production of haploid gametes. In most ferns both male and female gametes are produced on the same gametophyte. Because gametophytes

grow flat on the soil, sperm motility is readily effected through moisture accumulation, and eggs (which develop in vase-like structures similar to those of mosses) are fertilized with the result that zygotes are produced. As in mosses, only one zygote in a given gametophyte matures; it develops into an embryonic, diploid sporophyte, which eventually undergoes differentiation and forms roots, leaves, and a stem. Thus the cycle is completed when this plant matures and produces spores (Figure 8.17).

Although the life cycle of ferns is essentially like that of mosses, there is an outstanding difference in the relative duration and stature

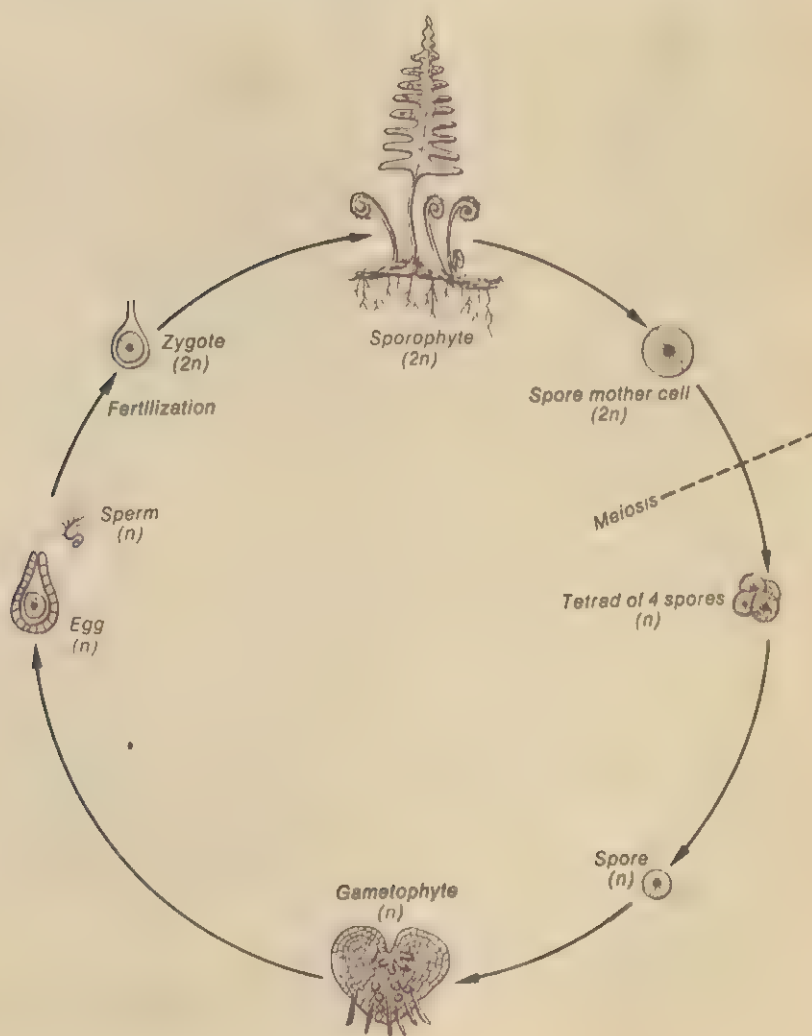


Figure 8.17 Life cycle of a fern.

of gametophyte and sporophyte. In the moss, the sporophyte grows upon the gametophyte, which is the dominant phase of the cycle. In contrast, it is the sporophyte of the fern that is the larger and more obvious plant, the gametophyte being small, insignificant, and short-lived. In fact, the gametophyte perishes and decays as soon as the sporophyte produced from it gains independence through root formation and chlorophyll development, whereas the sporophytic plant may persist for many years as a perennial.

Flowering plants By far the most numerous and successful plants on earth today (in number of species) are those which bear special organs of reproduction called flowers. It is a matter of simple observation that a great deal of variation exists in floral morphology among the different species of this group, but a close study of various flowers reveals a fundamental uniformity of structure.

Essentially, a flower is an aggregation of modified leaves, certain of which produce spores. In the typical flower, four types of structures are present: *sepals*, *petals*, *pistil(s)* and *stamens* (Figure 8.18). Although the flowers of most plants exhibit these four parts, there are some which lack one or more of them. The flowers of grasses, for instance, are devoid of sepals and petals as such. In certain species, pistils and stamens are borne in separate flowers. Corn (*Zea mays*), for example, bears staminate flowers at the top of the plant and those which are pistillate at a lower point (the "ear") on the stalk. Some species, such as willow and mulberry, even bear staminate and pistillate flowers on separate plants.

The process of reproduction is initiated in flowers when certain cells of the *anthers* (sporangia), located at the tips of stamens, differentiate into spore mother cells and undergo meiosis in the formation of haploid spores, which are called *pollen grains*. It is important at this point to realize that flowering plants (as well as the nonflowering seed plants), unlike most of the "lower" spore-producers, exhibit two kinds of spores which are different; one type, the pollen grain (*microspore*), is produced in the stamens, and the other type (*megaspore*) develops in the pistil. The pollen grains may be transferred to the tip of a pistil either of the same flower or to that of another flower belonging to the given species, depending upon circumstances. At this location, each pollen grain germinates and develops into a *pollen tube* which begins to grow downward through the pistil. Meanwhile, the base of the pistil, called the ovary,* undergoes changes associated with production of the second type of

*This term was ascribed to the structure by earlier botanists who did not fully understand its significance and who presumed it to correspond to the egg-producing organ of female animals. It is no longer regarded in this light, but the name still persists.

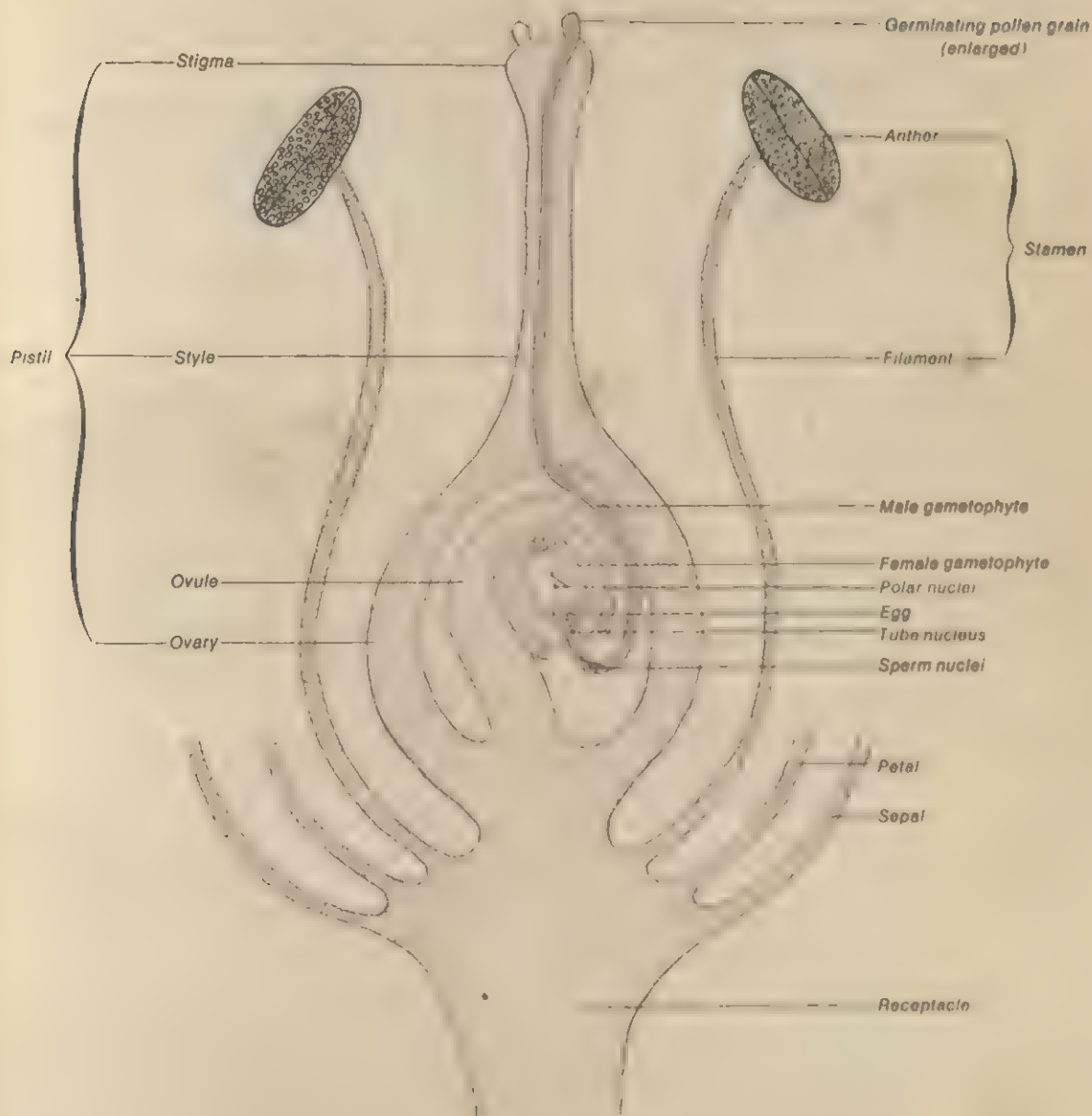


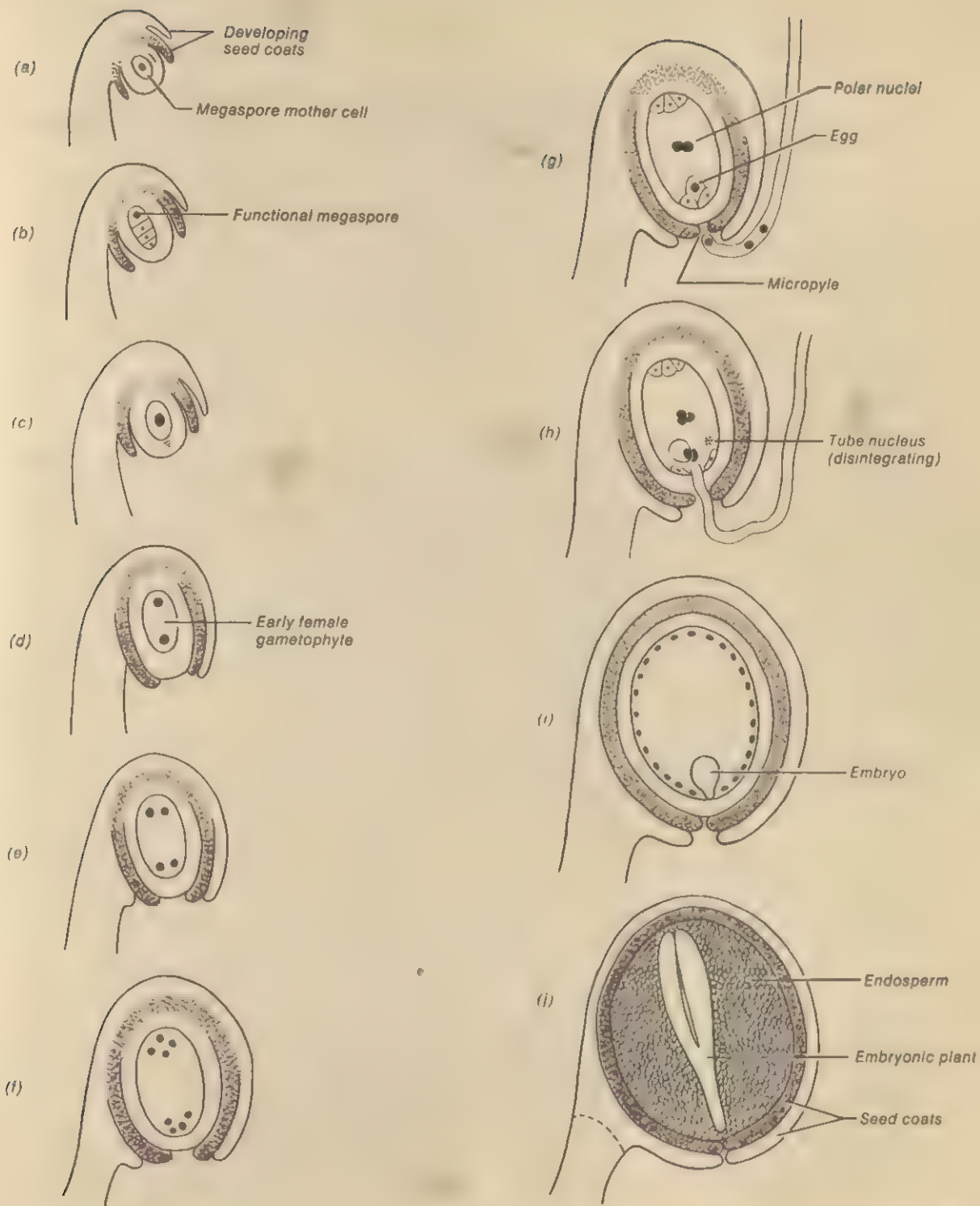
Figure 8.16 Diagrammatic representation of a typical flower at the time of fertilization. For purposes of simplicity, the ovary is shown as having only one ovule. In some species, such as peach or cherry, this is the case. It is more common to find a number of ovules within the ovary.

Figure 8.19 Typical development of female gametophyte within an ovule, with ultimate seed formation. (a) Young ovule with megaspore mother cell. (b) End of meiotic division of spore mother cell. Three megaspores are undergoing degeneration (c) Functional megaspore after a period of growth (d) End of first (mitotic) division of megaspore (e) Four-nucleate stage (f) Eight-nucleate stage (g) Fully developed female gametophyte, consisting of seven cells, the largest of which contains the two polar nuclei. Male gametophyte (pollen tube) now fully developed and approaching ovule (h) Discharge of two sperm nuclei into female gametophyte, double fertilization about to occur. Tube nucleus disintegrates. (i) Later development of ovule. Nuclear division has resulted in the presence of several endosperm nuclei, which have migrated outward. Embryo has begun its growth. (j) Fully developed seed, containing embryo with root and shoot. Endosperm nuclei have become enclosed by cell walls, and these cells now surround the embryo. Two seed coats have completed their development and form the outer coverings for the seed.

spore. Depending on the species, one or more *ovules*, which ultimately develop into seeds, undergo changes resulting in the formation of a deep-lying spore mother cell in each. This cell undergoes meiotic division, three of the four haploid products degenerate, and the nucleus of the other divides mitotically, eventually giving rise to eight nuclei. Cell walls form around six of these, one of which constitutes the egg cell. Two nuclei do not become enclosed by cell walls, and these are situated within the remaining cytoplasm. By this time, pollen tubes have grown down the pistil; one reaches each ovule, penetrates its tissues through a special passageway, the *micropyle*, and discharges two sperm nuclei in the vicinity of the egg. One of these unites with the egg, forming a diploid zygote, and the other fuses with the two free nuclei, forming a triploid ($3n$) nucleus (Figure 8.19). The remaining five cells play no further important role in development.*

From this point on, growth of the diploid embryo occurs with the formation of root and shoot. Meanwhile, the triploid nucleus has divided mitotically, and eventually it forms a nutritive tissue known as *endosperm*. The endosperm is ultimately utilized by the embryo, either before the latter enters the period of dormancy characteristic of seeds or after it renews its growth at germination. The outer tissues of the ovule form the *seed coats* which surround the embryo and endosperm (if any remains). A seed, therefore, is a special reproductive structure consisting of a dormant embryonic plant which is either surrounded by endosperm or filled with reserve food and covered by the outer portions of the ovule. Under proper conditions of moisture, temperature, and oxygen supply, and in the case of

*The foregoing account represents typical seed production in flowering plants, but it should be pointed out that certain deviations from this particular pattern are seen in some species.



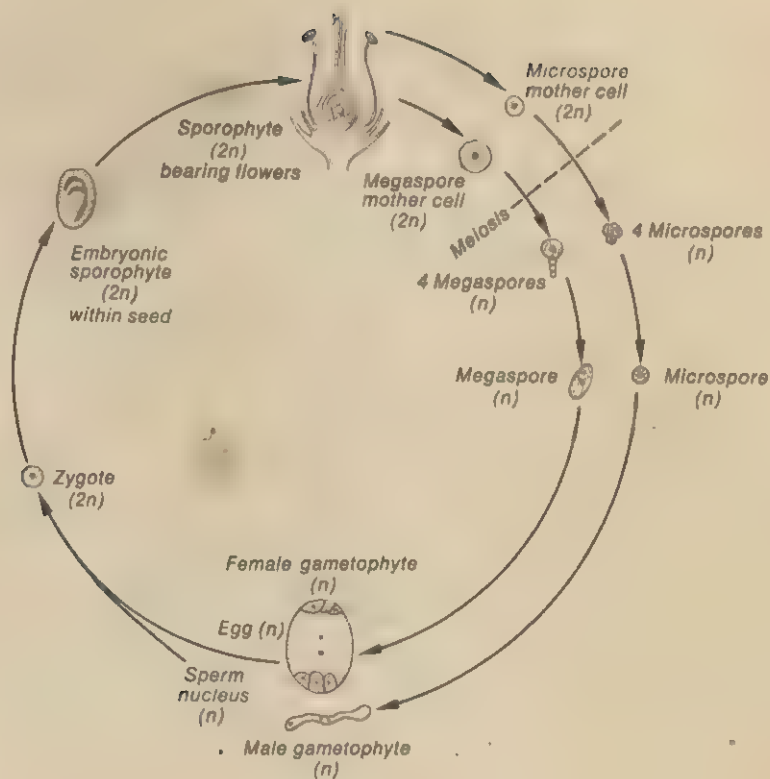
certain types after a necessary period of dormancy, the seed germinates with further development of the embryo and its ultimate establishment as an independent plant.

The ovary of the pistil with its enclosed seed or seeds matures into the *fruit*. It is popularly thought that a structure must be edible to be considered a fruit, but the ovaries of many flowers develop into fruits that cannot be used for food purposes. Furthermore, many fruits are considered to be vegetables; tomatoes, cucumbers, squashes, watermelons, and the pods of beans, for example, are all fruits by botanical definition. In consideration of edible plants, the question of whether or not a given portion is a fruit or a vegetable must be decided on the basis of its origin on the plant. If it develops from a floral ovary it is a fruit, and if it represents some other plant organ, it is a vegetable.

In terms of the life cycles exhibited by such plants as mosses and ferns, the flowering plant body must be considered the sporophyte, with male and female gametophytes being formed by the spores produced in stamens and pistils, respectively. The male gametophyte begins its formation when the nucleus of the pollen grain divides. One of the two resulting nuclei divides once more to produce the sperm nuclei, and the fully developed male gametophyte is merely a pollen tube with three nuclei. The female gametophyte is only slightly more complex at maturity, consisting as it does of seven cells. Thus, the gametophytic phase of the life cycle is greatly reduced in flowering plants (Figure 8.20).

An interesting question of sexuality arises in consideration of the two types of spores produced in flowering plants. It might seem logical to refer to pollen grains as male spores, and to consider those produced in ovules as being female since they give rise to male and female gametophytes, respectively. By the same reasoning, staminate flowers of corn might be considered male, and pistillate flowers would, of course, be female. To extend the concept further, species such as mulberry and willow would be made up of male and female trees. This application of sexuality is quite acceptable to some botanists, but it must be remembered that sporophytes are spore-producing plants, and that although spores are *potentially* male and female in flowering plants, they are still asexual in function, that is, with respect to the manner by which they produce the sexual phase. Although it is something of an academic question as to whether one can speak accurately of a male or female flower or plant, most botanists agree that sporophytic plants do not exhibit sexuality in the same sense that animals such as mammals do. Nevertheless, as we pointed out previously (Section 8.1), the spores of plants which exhibit dimorphic life cycles are produced by meiosis.

Figure 8.20 Life cycle of a flowering plant.



Thus, they are a part of a sexual process, and are certainly not asexual in the usual sense. If we consider genetic variability to be an expression of sexual reproduction only, then spores produced by meiosis certainly qualify.

In reviewing the plant groups which have been considered, it will occur to the student that they are much alike with regard to their sexual reproduction. Among other similarities, the phenomenon that alternating sporophytic and gametophytic phases of a life cycle appear in most plant groups, with sporic meiosis, is significant in its suggestion of a fundamental relationship between them. Similarly, most animals have a great deal in common with regard to reproduction; the exhibition of gametic meiosis, flagellated sperm, and relatively large, nonmotile eggs are a few of the features that indicate a basic similarity. Finally, sexuality and its accompaniments, so widespread in both kingdoms, add to the many other features which living forms generally share in common, allowing us to build toward some highly important generalizations which will be developed in a later chapter.

8.5 It might be inferred from the discussion to this point that new individuals arise from gametes only after their union, although an exception was noted in the development of drone bees from unfertilized eggs. As a matter of fact, gametic union is the rule in sexual reproduction, but the development of eggs that have not been fertilized, a phenomenon called *parthenogenesis* (Gr. *parthenos*, virgin + *genesis*, to be born) sometimes occurs. From the viewpoint of the biologist, this phenomenon is either *natural* (occurring in nature) or *artificial* (induced under laboratory conditions).

**The
phenomenon
of
parthenogenesis**

Natural parthenogenesis occurs to a considerable degree among insects, where certain species are known that do not feature male individuals at all; instead, females develop regularly from unfertilized eggs. In other species, such as the honeybee, only male individuals develop parthenogenetically. Parthenogenesis also is known among various other arthropods and in certain flatworms, as well as in a few algae such as *Ulva*, the sea lettuce. Among the vertebrates, it has been observed in turkeys. It undoubtedly occurs in a great many animal and plant species which have not been closely studied in this respect. Although there have been reports of natural parthenogenesis in humans, it is extremely doubtful that it ever occurs. Artificial parthenogenesis has been induced in a wide variety of animal forms including annelids, mollusks, echinoderms, amphibians, and even mammals. For example, frog eggs may be stimulated to develop by pricking them slightly with a needle that has been dipped in frog blood. Studies of artificial parthenogenesis have been very rewarding, showing as they have that one function of normal fertilization is the activation of division-initiating forces within the egg. If these forces are set off by chemical or mechanical means rather than by sperm entrance, then development may proceed more or less normally up to a point, even though the diploid chromosome number has not been restored. In some cases, fully developed animals may result from artificial parthenogenesis. However, in these cases, the diploid chromosome number is restored by some means.

You may wonder whether natural parthenogenesis is to be regarded as sexual reproduction inasmuch as there is no gametic union. Technically, of course, it is asexual, but since the individual arises from a cell that has undergone differentiation toward gametic union, many biologists regard parthenogenesis as being a highly unusual form of sexual reproduction. Certainly it fails to conform to our previous definition of sexual reproduction, but since one specialized sex cell is involved, it would be difficult to regard it in the same light as somatic reproduction or spore germination. Actually,

good arguments can be made for either viewpoint, and perhaps it is best to consider parthenogenesis a type of reproduction which involves both sexual and asexual features.

8.6 An introduction to genetics

When individuals are produced whose characteristics are essentially like those of the other members of their species, it is obvious that inheritance is manifested. The field of genetics has developed within biology through a study of the forces involved in the transmission of traits from parents to offspring, and a great deal has been discovered about the mechanisms which are involved.

It should become obvious as we consider genetic mechanisms that variability is a fundamental characteristic of sexual reproduction. We have seen that meiosis segregates chromosomes in the formation of gametes and spores, but we have not followed through on the genetic implications of this segregation. Similarly, we have suggested that gametic union with its consequent association of chromosomes from different parents is a mechanism which produces variability through new genic combinations. Because it is very difficult to understand genetic mechanisms without some knowledge of sexual reproduction and its implications, we have chosen in this book to consider both subjects within a single chapter. From this viewpoint, our discussion thus far provides a background for understanding genetic mechanisms, and in turn, a discussion of genetics will give meaning to reproductive mechanisms.

The work of Gregor Mendel Before the middle of the nineteenth century, practically nothing was known about inheritance except that it occurred. At this time, an Austrian monk, Gregor Johann Mendel (1822-1884), began a series of experiments which served as the basis for a clarification of elementary genetic principles. Mendel was not a scientist by vocation, although he did teach various sciences for many years in the *Realschule* (comparable to the American high school) of what was then Brunn, Austria. He developed a great curiosity about inheritance and conducted experiments independently in a monastery garden. Following many years of experimentation involving a variety of cultivated plants, Mendel reported his results and conclusions in 1865, followed by their publication as a paper during the next year. Unfortunately, the biological world was not ready for Mendel's findings and did not fully appreciate them until the year 1900, when his paper was rediscovered and compared with cytological knowledge that had developed since Mendel's time. Thus it was never known to him or to his contemporaries that he had made one of the greatest scientific contributions of all time through the formulation of certain elementary genetic principles.

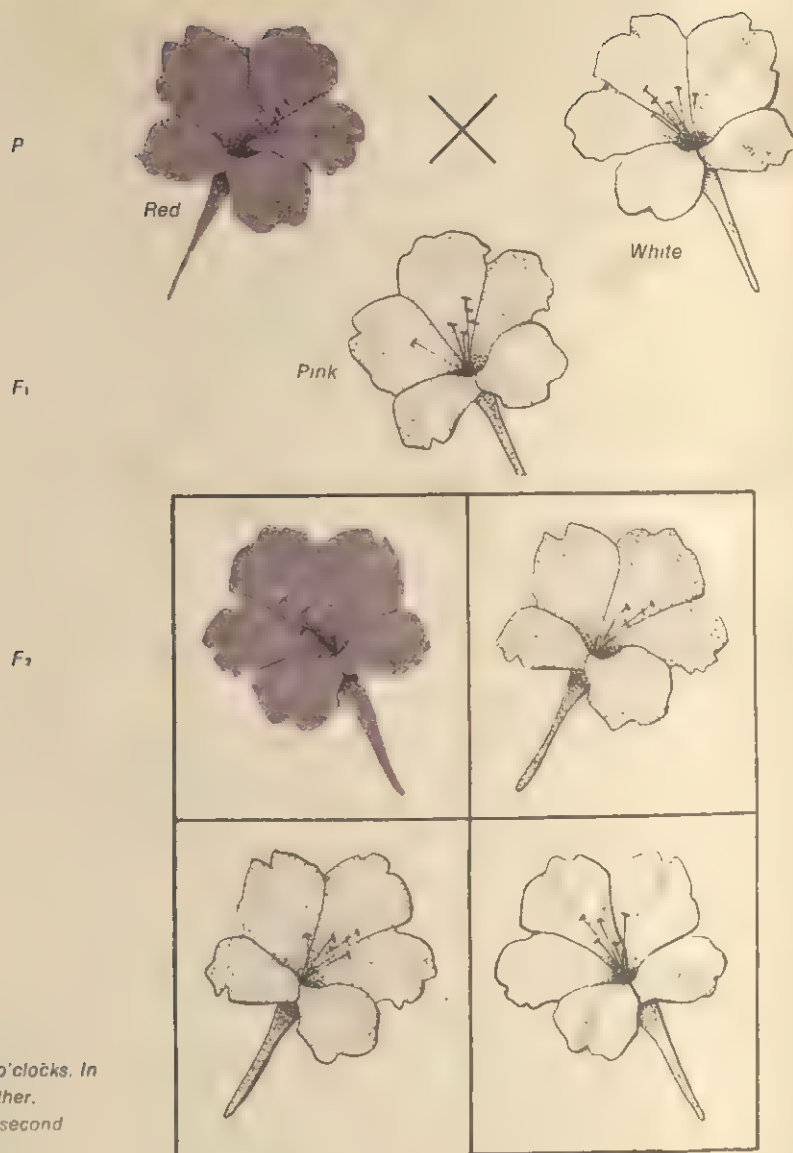


Figure 8.21 The "blending" of traits in four-o'clocks. In this case, neither gene is dominant over the other. P, parental types; F₁, first filial generation; F₂, second filial generation, obtained by crossing F₁ × F₁.

It was common in Mendel's day to regard inheritance as the result of a blending of traits since it was known that something of this sort occurred in the crossing of certain varieties within plant or animal species. In the four-o'clock (*Mirabilis jalapa*), for example, red-flowered plants produce nothing but more red-flowered plants when crossed only among themselves, and white-flowered plants likewise breed "true" for white flowers. However, when pollen from either a

red- or a white-flowered plant is transferred to the pistil of the other type of flower, the seeds which are formed by this cross produce pink-flowered plants. Thus a blending of traits could readily be seen. It disturbed Mendel that pink-flowered plants of this sort never bred true, as should be the case if a simple blending were responsible; this inept theory of inheritance failed entirely to explain why hybrids (offspring of parents which differ in a given trait) often revert back to parental types. For example, the offspring of two pink four-o'clocks may be white, pink, or red (Figure 8.21). It was equally disturbing to him that this sort of reversion occurred in crosses where no blending was obvious but where a hidden trait kept cropping out.

The monohybrid cross. For his experimental work, Mendel relied chiefly upon the garden pea (*Pisum sativum*), which he knew to include several true-breeding varieties that could readily be crossed with each other. Some of these varieties were quite tall and had to be trained as vines, while others were extremely short. Other contrasting traits were seed colors (green or yellow), seed form (round or wrinkled), and flower positions (borne along the main stem or in a group at the top of the stem). In all, he worked with seven pairs of contrasting traits in this species. As it turned out, no blending of traits occurred; for example, seeds resulting from a cross between tall and short peas did not produce plants which were intermediate in height, but rather, all of them were tall. Mendel referred to that trait which appeared in the hybrid as being "dominant" and the one which did not appear as "recessive." Hence, tallness proved to be the dominant trait in the cross just cited, and shortness was recessive to it.

At this point, Mendel took a very important step. He allowed hybrids for a given pair of traits to self-pollinate, and he analyzed the results of his seven separate experiments. In each case, individuals showing the recessive trait appeared and in definite numerical ratio to individuals exhibiting the dominant trait. *Without exception, in this second generation, a ratio of approximately three dominants to one recessive appeared.* For example, Mendel produced 1,064 plants in the tall-short experiment, of which 787 were tall and 277 were short. A still further extension of the general experiment revealed that in all seven groups, the individuals showing recessive traits bred true for them, one-third of the dominant individuals likewise bred true, and the remaining two-thirds of the dominants did not.*

It seemed to Mendel that more was involved here than met the eye, and he postulated the existence of "characters" which were associated with the gametes of parent individuals. By allowing letters of the alphabet to represent these characters, he was able to manip-

* Since it was a simple matter to ensure that the flowers were self-pollinated, it was relatively easy for Mendel to test the genetic "purity" of any given plant.

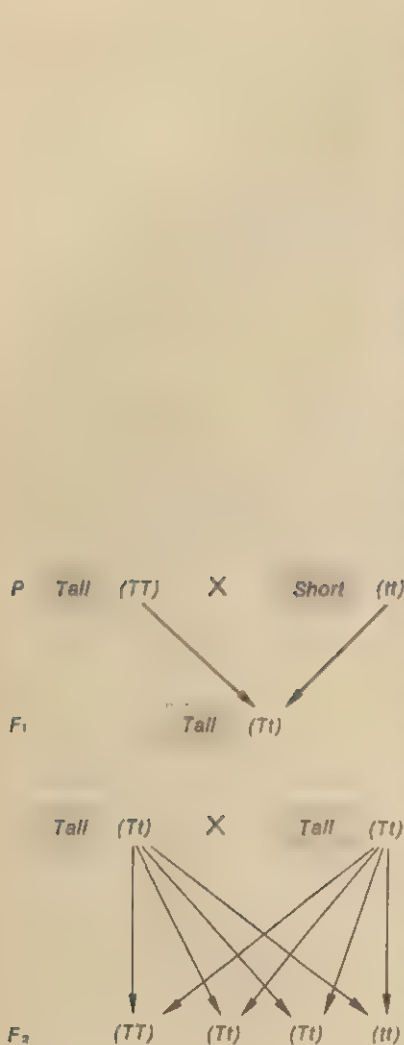


Figure 8.22 A representation of theoretical results from two generations of crossing tall and short peas. It should be borne in mind that Mendel postulated the inclusion of one and only one character (gene) of a given pair within a gamete. The parental plants can produce only one type of gamete each; hence they produce only one type of offspring when crossed. The F_1 plants, however, can produce two types of gametes each, and they produce four classes of offspring, two of which are identical in type.

ulate them theoretically and thus to set up his crosses on paper. For the sake of convenience, capital letters were made to represent dominant characters, and small ones were used for recessives, a system which is still employed in genetics. On this basis, Mendel came to the conclusion that only if the genetic constitution of a parent plant were represented by two characters for a given trait, with one and only one of these being transmitted to a gamete, could his results be explained. Hence, in the crosses involving tall and short peas, where the contrasting parent plants were pure for their traits, the hybrids are mixed with regard to their genetic characters. A cross between two such hybrids, in which random combination of gametes occurs, results in one individual pure for the dominant characters, one pure for the recessive ones, and two which are mixed out of every four produced. Because of dominance, three of the four will exhibit the dominant trait (Figure 8.22). You will recall that this agrees perfectly with Mendel's experimental results. Furthermore, it explains the situation in such cases of inheritance as that of four-o'clocks, if it be assumed that neither of the characters involved is dominant over the other (Figure 8.21).

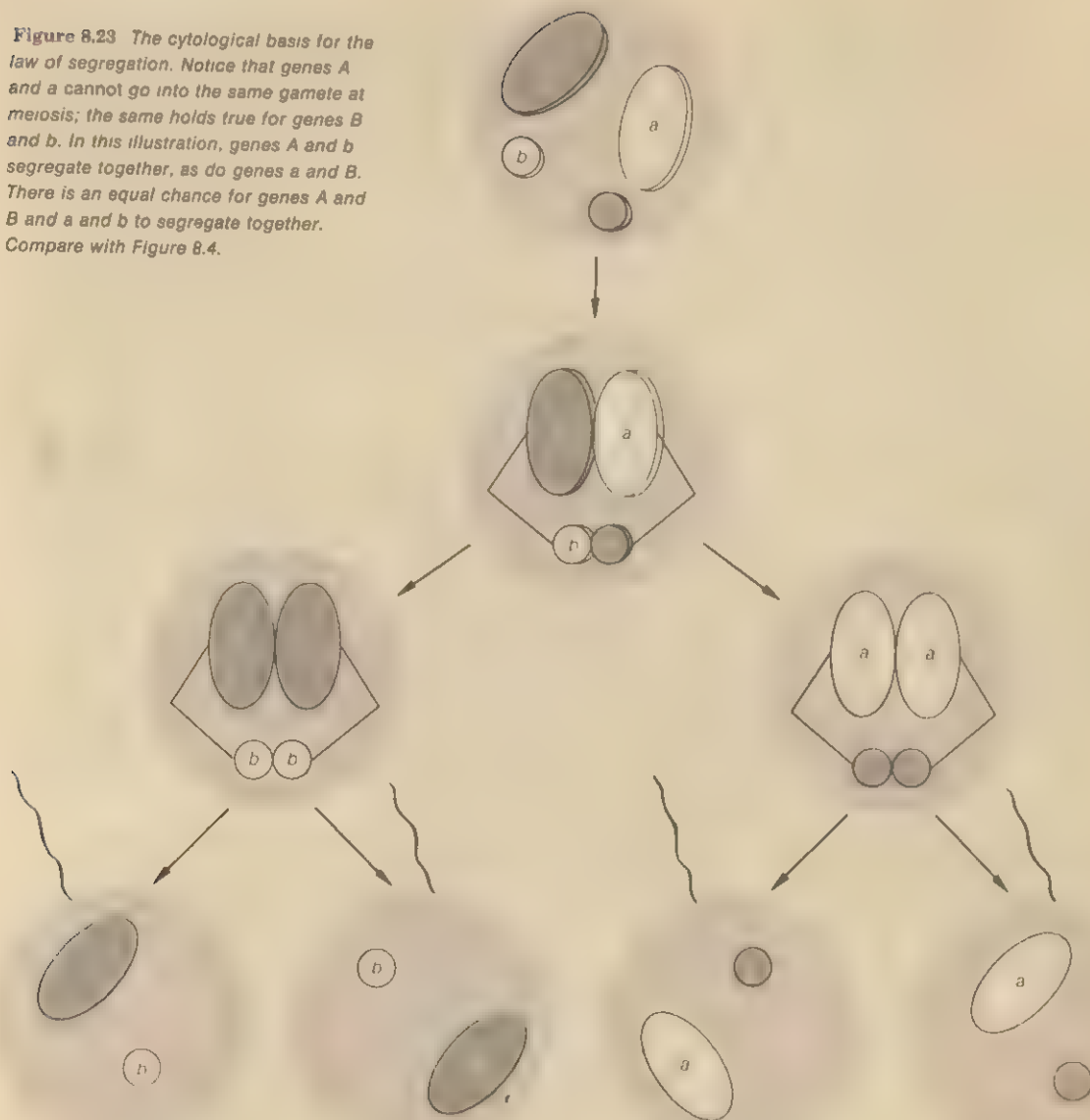
Since Mendel's time the term *gene* has replaced *character*, and it has been shown that genes are closely associated with chromosomes, being in some fashion a part of their chemical structure. Let us note at this point that Mendel was completely unaware of the existence of chromosomes: they were not observed until about 1870. Mitosis was elucidated a few years later, and meiosis was described in the early 1880's. Mendel's concept of the gene (although he did not use this term) therefore preceded the discovery of chromosomes. In 1903, the cytologist W. S. Sutton pointed out the parallelism between Mendel's "characters" and chromosomes with regard to gamete formation.* In his paper of 1866, Mendel postulated a "law of segregation," which states that *during gamete formation, each member of a pair of genes becomes associated with a different gamete*. Let us note that this is exactly what happens to homologous chromosomes in the meiotic process of animals (Figs. 8.4, 8.5, 8.23).†

Since chromosomes are segregated into different gametes, it follows that whatever genes they carry are also segregated, with equal numbers of gametes being formed for each gene type when members of a gene pair are not identical. This is a beautiful example of

* For an abridged version of Sutton's paper, see Gabriel and Fogel (reference at the end of Chapter 1).

† When meiosis is either zygotic or sporic, as in most plants, the law of segregation still holds. Genes are merely segregated much earlier in terms of gamete formation than is the case in gametic meiosis.

Figure 8.23 The cytological basis for the law of segregation. Notice that genes *A* and *a* cannot go into the same gamete at meiosis; the same holds true for genes *B* and *b*. In this illustration, genes *A* and *b* segregate together, as do genes *a* and *B*. There is an equal chance for genes *A* and *B* and *a* and *b* to segregate together. Compare with Figure 8.4.



the way science grows: Mendel's genius lay in his ability to manipulate hypotheses, theories, and data in such a fashion that his conceptual schemes became exceedingly fruitful at a later time. In fact, there are very few scientists whose conceptual schemes have been more significant and far-reaching than those of Gregor Mendel, and it is supremely ironic that he was not even regarded as a scientist by his contemporaries!

Reproduction

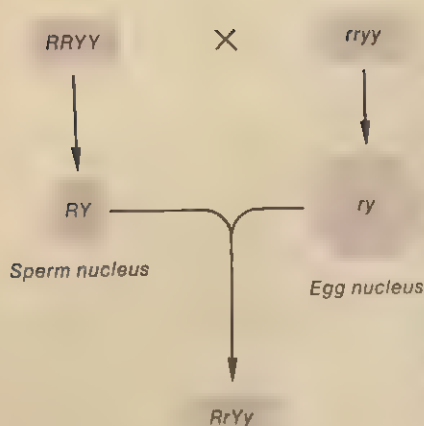


Figure 8.24



Figure 8.25

Sperm nuclei	Egg nuclei			
	RY	Ry	rY	ry
RY	$RRYY$	$RRYy$	$RrYY$	$RrYy$
Ry	$RRYy$	$RRyy$	$RrYy$	$Rryy$
rY	$RrYY$	$RrYy$	$rrYY$	$rrYy$
ry	$RrYy$	$Rryy$	$rrYy$	$rryy$

Figure 8.26

At this point, let us consider a few terms that are commonly used in genetics. In describing the genetic constitution of an organism for a given trait, the term *genotype* is used. Hence, the genotype for a pure-breeding tall pea is TT , that for a pure-breeding short one is tt , and the hybrid is Tt . The term *phenotype* is used to describe a genetic trait as it is detected by our senses. Thus, a plant from the same example whose genotype is either TT or Tt is phenotypically tall. Whenever members of a gene pair are identical, as in the genotype TT , the individual is said to be *homozygous* with regard to these genes. If the members differ, as in the genotype Tt , it is said to be *heterozygous*. Members of the same gene pair which differ in their genetic expression, such as T and t , are called *allelic genes*, or simply *alleles*.

The dihybrid cross On the basis of the law of segregation, let us predict what results could be expected if *two* pairs of contrasting characters (genes) were crossed. Again using the pea as an example, it will be recalled that Mendel found that round seed shape dominated wrinkled and that yellow color dominated green. If a pure-breeding plant which bears round, yellow seeds were crossed with one bearing wrinkled, green seeds, the situation might be symbolized as follows: $RRYY \times rryy$.

Because of genic segregation, the hybrid seeds should be *phenotypically* identical to those of the parent which was characterized by round, yellow seeds, but *genotypically* we would predict that they should be heterozygous for both gene pairs, as is shown in Figure 8.24.

When two plants produced by such hybrid seeds are crossed (or one plant is allowed to self-pollinate), four types of sperm nuclei should be formed, as well as four types of egg nuclei, with regard to genotype, as is shown in Figure 8.25.

We illustrate in Figure 8.26 the possible combinations that may occur when this cross is made.

Genotypically, several combinations would thus occur, but let us notice the theoretical *phenotypic* results. Of every sixteen seeds formed, on the average we should observe the distribution shown in Figure 8.27.

Mendel performed this very cross, and produced 556 F_2 seeds, as follows:

- 315 round, yellow
- 108 round, green
- 101 wrinkled, yellow
- 32 wrinkled, green

Since this is a 9:3:3:1 ratio, allowing for some chance variation, it

Figure 8.27



provided Mendel with very good evidence that his law of segregation was valid. Furthermore, he carried the experiment further by testing the F_2 seeds for genotype, which was accomplished by planting them and allowing the resulting plants to self-pollinate. His results substantiated, in general, the theoretical expectation.

From these and other experiments, Mendel was able to formulate a second important generalization, the *law of independent assortment*, which applies to genes of unlike pairs in their association within the same genotype. It should be obvious from the experiment discussed above that neither gene pair influences the other in any way. Taken separately, each produces a 3:1 phenotypic ratio in the F_2 generation, even though the experiment involves both pairs. Stated more precisely, *the law of independent assortment holds that a given gene pair segregates independently of any other gene pair in the formation of gametes*. When we trace out the possible fates of genes and their chromosomes during meiosis, it is readily seen why this "law" is operative (Figure 8.23). It should be remembered, however, that Mendel arrived at both his first and second laws through experimentation and statistical analysis and that it was many years before the cytological basis for their validity was known.

Intergenic linkage By definition, the law of independent assortment can apply only when gene pairs are located on different chromosomes. Let us compare the inheritance of two hypothetical genes, *A* and *B*, when they are independent (located on different chromosome pairs) and when they are linked (located on the same chromosome pair). It can be shown by diagram that genes located on the same chromosome are obliged to become associated *together* in a gamete and that there is no independent assortment (Figure 8.28). In fact, assuming that no interchange occurs between the chromosomes, it would appear that only one pair of genes is involved, since a 3:1 ratio is obtained.

It is interesting to note that the species of pea with which Mendel worked is characterized by seven pairs of homologous chromosomes and that he studied seven different traits, all of which showed independent assortment. Had he considered an eighth trait, it would

Independent

Linked

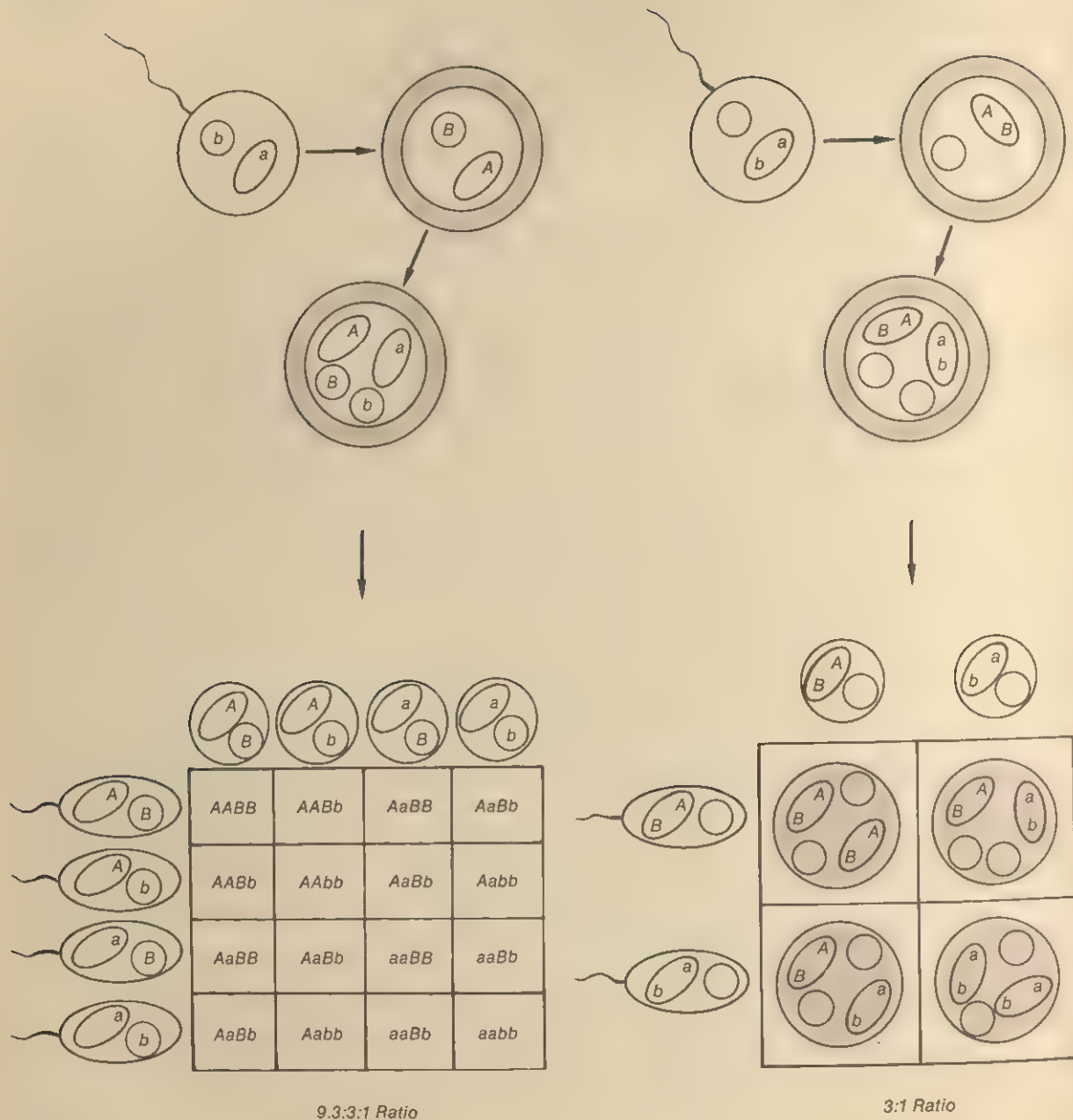


Figure 8.28 A comparison of independent assortment and linkage. In an actual cross, would you expect a 3:1 ratio in the F₂ if the two genes involved were linked? Explain.

necessarily have segregated with one of the other seven. Thus he would have observed an exception to his typical 9:3:3:1 ratio in the dihybrid cross, which would have necessitated a further qualification of the law of independent assortment. For example, a trait Mendel did not study is the presence or absence of tendrils (modified leaves which serve as holdfasts). The gene controlling the presence of tendrils is dominant to that which is related to their absence. Let us consider a cross between a pea plant with tendrils, bearing round seeds, and a plant without tendrils which bears wrinkled seeds (Figure 8.29). Obviously, the typical 9:3:3:1 ratio characteristic of independent assortment does not appear in this cross, and there are far more parental types than recombinants among the F_2 . Thus we might conclude tentatively that these genes are linked. However, it is evident that intergenic linkage is not complete, since the two recombinant types (round, no tendrils and wrinkled, tendrils) appear in small numbers. If one compares the number of round with the number of wrinkled individuals, it is apparent that there is an approximate 3:1 ratio (323:126) as expected. The same is true of the ratio between plants with tendrils and those without tendrils (321:127). Thus the alleles of each pair of genes apparently segregated from each other with dominant and recessive genes appearing in a 3:1 ratio. However, the two sets of alleles did not segregate independently of one another, nor did they segregate in a completely dependent manner. Therefore, if these two allelic sets are linked, the linkage is not complete.

From the purely genetic evidence of this cross, there appears to have been some interchange of material between homologous chromosomes giving rise to a few gametes containing recombinations of linked genes. Other explanations could be made for these data, but when all possibilities are considered, this one emerges as

P	Round, tendrils <i>RrTt</i>	X	Wrinkled, no tendrils <i>rrtt</i>
F_1	Round, tendrils <i>RrTt</i>		
$F_1 \times F_1$	Round, tendrils <i>RrTt</i>	X	Round, tendrils <i>RrTt</i>
F_2	Round, tendrils	319	
	Round, no tendrils	4	
	Wrinkled, tendrils	3	
	Wrinkled, no tendrils	123	

Figure 8.29 A cross involving two pairs of linked genes. In this case, linkage is not complete (that is, crossing over occurs). Compare with Figure 8.28. As an exercise, diagram this cross in the fashion of Figure 8.28.

the simplest and the most logical. In fact, cytological evidence supports this explanation. You will recall that in our discussion of meiosis (Section 8.2) we pointed out that during synapsis an exchange of parts may occur between chromatids of different homologous chromosomes (Figure 8.4). Thus, such an exchange as we have postulated on the basis of genetic evidence does indeed occur. Cytological examination of synapsing chromosomes reveals that exchanges involving any particular point on a chromosome do not occur in every meiotic event, but only in some. This accounts, at least in part, for the relatively small number of recombinant gametes which combine and produce recombinant offspring. In fact, the percent of exchange (crossing-over) is relatively constant when two particular traits are considered, and genes may actually be mapped with fair precision with regard to their location within chromosomes.

It should be apparent from this discussion that crossing-over of genes from one member of a pair of homologous chromosomes to the other during meiosis contributes to variability in gametes and offspring. The random distribution of chromosomes alone in the formation of gametes (Figure 8.4) provides almost unlimited opportunity for variation from parental types; when the two sources of variability are added together, the significance of meiosis and sexual reproduction becomes impressive indeed. In a later chapter, we shall consider how genetic variability originates, and how it plays an important role in the process of evolution.

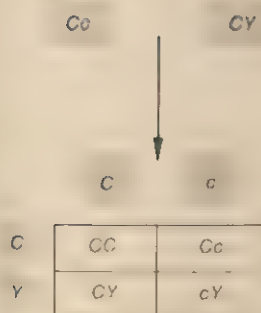
Sex determination and sex linkage Since Mendel's time, it has been found that in many plants and animals, the sex of offspring is determined by the inheritance of a certain chromosomal complement. For example, there are normally twenty-three pairs of chromosomes in the body cells of the human, twenty-two of which consist of morphologically identical members. In the female, the other pair also consists of like chromosomes, but in the male the two members of this pair are both morphologically and genetically dissimilar. For purposes of distinction, biologists refer to members of the twenty-two pairs as *autosomes*, and to members of the twenty-third pair as *sex chromosomes*. The male, of course, possesses one sex chromosome which females do not carry, and because its shape in certain animals that were used in early work on this aspect of genetics is something like that of the letter Y, it is called the *Y-chromosome*. Its partner sex chromosome in the male is called an *X-chromosome*; the female, of course, possesses a pair of these. Hence, male and female individuals differ with regard to their sex chromosomes.

At the time of sperm formation in the testes of the male, the sex chromosomes undergo segregation as do the autosomes. Thus, it is a matter of chance as to whether the X-chromosome or the Y-chro-

mosome go into a particular sperm, but it should be clear that both cannot be carried to the egg by a single sperm. The inheritance of sex depends upon whether an X-bearing sperm or a Y-bearing one fertilizes the egg. The problem of sex determination actually is a complex one involving many factors, but the initial step in the process is the combination in the zygote of either two X-chromosomes (resulting in female sex) or of an X and a Y (resulting in male sex).

Now let us postulate that since the X- and Y-chromosomes differ morphologically, they might be expected to bear genes that are not homologous. As a matter of fact, the Y-chromosome bears few if any genes, whereas the X-chromosome is known to carry a large number. Because genes located within the X-chromosome of a male do not have alleles, the inheritance pattern of these genes is greatly affected. For example, a gene is known to reside on the X-chromosome of the human which controls normal color vision. Its recessive allele, when effective, interferes with the ability characteristic of most people, to distinguish between certain colors. Possible genotypes and phenotypes of persons in regard to these genes are as follows, allowing the letter Y to represent the absence of any gene at all, since the Y-chromosome carries none for this trait:

- CC normal (homozygous) female
- Cc normal (heterozygous) female
- cc color-blind female
- CY normal male
- cY color-blind male



- CC normal (homozygous) female
- Cc normal (heterozygous) female
- CY normal male
- cY color-blind male

Since the production of a color-blind female depends upon parents each of whom can contribute a recessive gene, females exhibiting the abnormality are somewhat rare. On the other hand, color-blind sons (but no color-blind daughters) can be produced by a normal man and a heterozygous woman as shown in Figure 8.30. For this reason, most individuals who exhibit recessive traits dependent upon *sex-linked* (located on a sex chromosome) genes of this sort are men. Perhaps by a manipulation of genotypes, you will be able to determine why such traits appear to skip characteristically from maternal grandfather to grandson.

In addition to their significance with regard to sex determination and sex-linked inheritance, sex chromosomes are of interest to biologists in another respect. They provide strong support for the theory that genes are associated with chromosomes, since alternate hypotheses purporting to explain inheritance are difficult to reconcile with the observations and experiments involving sex-linkage and sex determination. This may not be readily apparent, since we have taken a gene-chromosome theory for granted throughout most of

Figure 8.30

our discussion, but in the early days of genetic research the sex chromosomes were of tremendous theoretical significance. Although there are other lines of evidence which indicate the gene-chromosome relationship in organisms, perhaps the data from experiments involving sex chromosomes are the most conclusive of all. In other words, the hypothesis that genes are localized within chromosomes receives strong confirmation from the data regarding sex determination and the inheritance pattern of such genes as those associated with color-blindness. The gene-chromosome theory then is a fruitful conceptual scheme to use Conant's terms, and it has given rise to a limitless expansion of observation and experimentation.

The action of genes. Although the true nature of the gene is not yet fully understood, it appears that it somehow operates as a discrete chemical unit or determiner of traits. It is now known that DNA is the actual genetic material of cells, and we have already seen (Chapter 5) how DNA controls synthesis in the cell. Apparently a given gene (or DNA unit, in biochemical terms) is a certain fraction of a DNA molecule which serves as a master pattern, or template, from which RNA duplicates are made (Figure 5-5). These duplicates (messenger RNA molecules) travel from the nucleus to the ribosomes, where they control protein synthesis, and it is the specificity of these proteins (which may function as structural components of new cells or as enzymes) that imparts to the organism its characteristics. Thus, when we call attention to a difference between a given gene *A* and its recessive partner *a*, we are only giving meaningful expression to what is perhaps the ability of one gene to influence the production of some enzyme which is not produced under the influence of the other. Presence or absence of this enzyme in cells then possibly leads to some visible or functional difference in the organism. Besides serving as the template for production of proteins, the gene is capable of producing still other templates, like itself. This occurs during the interphase preceding cell division.

Perhaps an example of genic action on the molecular level will serve to emphasize the principle that genes work through biochemical and physiological channels. The blood pigment hemoglobin, which is a protein, has a definite chemical structure; a molecule of hemoglobin is composed of about 8,000 atoms, with most of these being contained in some 600 amino acid molecules. An abnormality of the human called *sickle-cell anemia* (Figure 8-31), which is a so-called genetic disease, is actually a manifestation of abnormal hemoglobin. Biochemists have determined that normal hemoglobin and sickle-cell hemoglobin differ only in a single amino acid on each side of the molecule, which is a sort of "double" structure. The amino

8.7 In view of the fact that organisms are not immortal, reproduction is a necessary expedient to the survival of species. Essentially, there are two types of reproduction, sexual and asexual. Sexual reproduction is characterized by meiosis and chromosomal recombination, whereas asexual reproduction is not characterized by these mechanisms of variability. This difference in these two distinct modes of reproduction has profound implications for genetics and evolution.

Summary

Although patterns of reproduction among animals vary considerably in specific detail, certain essential features are common to all, especially with regard to sexual reproduction. For example, meiosis is gametic in all animals. Asexual reproduction is largely restricted in the animal kingdom to the less complex forms. In order to demonstrate patterns of reproduction at a variety of levels in the animal kingdom, we have discussed reproduction in *Paramecium*, *Hydra*, the earthworm, the honeybee, the frog, and man. As in animals, plants show a variety of reproductive patterns, although here, too, there are certain features which appear at all levels of complexity. In contrast to animals, most plants exhibit sporic meiosis, although some of the less complex forms are characterized by gametic or zygotic meiosis. Also in contrast to animals, asexual reproduction is featured by some of the more complex seed plants. We have discussed reproduction in *Chlamydomonas* (a green alga), a moss, a fern, and a flowering plant.

Because our approach to the subject of genetics relies upon a background knowledge of meiosis and other mechanisms which control variability, this subject is reviewed in the light of sexual reproduction. The work of Gregor Mendel in the nineteenth century clarified the basic principles of heredity, although it was not until the twentieth century that these principles made an impact upon biology. Since that time, genetics has pervaded all areas of biology, especially within recent years when genes and genetic mechanisms have been interpreted in biochemical terms.

Questions

1 Define the following terms: copulation, monoecious, fetus, spore mother cell, parthenogenesis, phenotype, synapsis, gametophytic phase, fruit, genetic linkage.

2 What do you consider the fundamental difference between sexual and asexual reproduction?

3 In your view, what is the fundamental difference between mitosis and meiosis? How is chromosomal behavior related, in each case, to the biological role of the process?

4 What are the essential differences among gametic, sporic, and zygotic meiosis? Cite a life cycle characterized by each of these meiotic types.

5 Asexual reproduction is limited almost entirely in the animal kingdom to the least complex animals, whereas many of the most complex plants reproduce in this fashion with regularity. Can you account for this seeming contrast in terms of biological significance?

6 In what ways is sexual reproduction in *Paramecium* somewhat atypical? In *Chlamydomonas*?

7 A female frog usually produces several hundred eggs in a single season, all of which may be fertilized and develop into frogs. In contrast, a human female may produce only a few eggs in a year's time, and at most, could bear only about one child per year. In spite of this difference in reproductive potential, the human species is increasing at an alarming rate while there are probably fewer frogs in the world with each passing year. How can you account for this?

8 Botanists differ somewhat among themselves as to whether the spores of seed plants are sexual or asexual reproductive bodies. Could you defend either viewpoint?

9 A certain teacher gave a test which included this item: "Discuss sexual reproduction in flowering plants." A part of one answer went this way: "In flowering plants, the pollen grains are the sperm cells and the ovules are the eggs. These unite and form a zygote, which develops into a seed." What criticisms can you make of this answer?

10 Define the "law of segregation" and the "law of independent assortment." How is each related to the events of meiosis?

11 Gregor Mendel was almost totally unappreciated as a scientist during his lifetime, yet today he is generally regarded as one of the most illustrious men in the history of science. How can we account for this?

12 Discuss the brief definition given for genetics as "DNA in action." What are some of the mechanisms, or channels, by means of which DNA exerts genetic effects?

13 In man, the gene for red hair (regardless of shade) is apparently recessive to all other "hair-color" genes. A brown-haired man and a blond woman produce a red-haired child. Which of the following statements is acceptable in view of the evidence? (a) One of the woman's parents was red-haired; (b) one of the man's parents was red-haired; (c) the child is heterozygous in genotype; (d) both parents are heterozygous in genotype; (e) only one of the parents is heterozygous in genotype; (f) the next child of this couple will not have red hair.

14 In man, the gene which controls normal pigmentation (A) is dominant to the gene which controls albinism (a). A certain man with normal pigmentation married three times. His first wife was an albino, and they had a normally pigmented son. His second wife was also an albino and they had an albino daughter. His third wife was normally pigmented, and they had one normally pigmented son and one albino daughter. Write the genotypes of all these individuals. There is one individual in the group whose genotype you cannot ascertain. Which one is it?

15 In cattle, the polled (hornless) condition is dependent upon a gene H , and the horned condition is dependent upon its recessive allele h . A cross between red (R) and white (r) results in roan (Rr), that is, there is lack of dominance (see the inheritance of four-o'clocks in this chapter). A polled, red bull is mated to three cows. With cow A , which is horned and white, a polled, roan calf is produced. With cow B , which is horned and roan, a horned, red calf is produced. With cow C , which is polled and red, a horned, red calf is produced. What are the genotypes of all individuals? Let us suppose the calf produced from cow A is a male, and is eventually mated to several cows of his own genotype. How many roan, polled calves should be produced out of sixteen?

16 In guinea pigs, the gene for black coat (B) is dominant over that for white coat (b), and the gene for rough coat (R) is dominant over that for smooth coat (r). A black, rough guinea pig is mated to a white, rough one. Out of several litters totaling 22 individuals, 8 are black and smooth, 7 are white and rough, and 2 are white and smooth. What are the genotypes of the parents?

17 A rough, black male is mated to several smooth, white females. Out of a number of litters, offspring are as follows: 18 rough, black; 21 rough, white; 16 smooth, black; 24 smooth, white. If this male had been mated to another guinea pig of identical genotype to his own, what proportion of their offspring would have been rough, white? (a) 1 out of 4, (b) 1 out of 16, (c) 3 out of 16, (d) 6 out of 16, (e) 9 out of 16.

18 In the human, color blindness is dependent upon a recessive sex-linked gene c . Normal vision is represented by C . A color-blind man marries a woman with normal vision. Which of the following can be said with confidence? (a) They can have no color-blind sons; (b) none of this man's daughters can be free of a color-blind gene; (c) the man's father was color blind; (d) the man's mother was color blind; (e) the man's mother was heterozygous in respect to color blindness.

19 A man with normal vision marries a woman with normal vision. Her father was color blind. What are the genotypes of these

three individuals? What genotypes and phenotypes may appear among the children of this couple?

20 A red-haired, color-blind man with normal pigmentation married a brown-haired woman with normal vision and normal pigmentation. The genes which control these three traits are identified with three different chromosome pairs. Four children were born to this couple, as follows: a red-haired son with normal vision and normal pigmentation; a blond, albino daughter with normal color vision, a brown-haired, color-blind son with normal pigmentation; a brown-haired, color-blind daughter with normal pigmentation.

a Using A and a for pigmentation, C and c for vision, and R and r for hair color, express the genotype of the man with regard to these three traits.

b Express the genotype of the woman with regard to these three traits.

c Express the genotypes of all the children with regard to these three traits. (Note. *Each child* has one trait out of the three concerning which the genotype cannot be stated from the data given. Note this trait in each case.)

d If this couple has another child, what is the probability that it will be an albino? That it will be a color-blind boy? That it will be a redhaired, color-blind girl? (Disregard the possibility in this last case that the child will be albino).

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Responsiveness

It is a matter of common knowledge that higher animals possess senses that enable them to respond to stimuli. Man, for example, is able to see objects, hear sounds, feel pain, and so on. This ability to respond to such stimuli is not limited to the more complex animals, however. If an amoeba is brought into contact with light, heat, or the tip of a pointed object, it will withdraw from the source of irritation. Indeed, plants are sensitive to many stimuli (Figure 9.1), although in the case of forms that do not exhibit motility, this may not be immediately apparent. The capacity to respond to stimuli is called *responsiveness*, and it is characteristic of all organisms to at least some extent.

Of course, nonliving substances or materials may exhibit responsiveness to a certain degree, just as chemical activity and increase in total mass are not limited to organisms in their characteristics of metabolism and growth. Here again, however, there is a considerable difference in the degree to which this may occur. The element mercury, for example, is highly responsive to changes in temperature, and for this reason it is utilized in thermometers, thermostats, and similar instruments. The art of photography is made possible through the sensitivity of certain chemicals to light. However, such physical and chemical changes are relatively simple and easy to explain, whereas responsiveness in even the least complex of living organisms is a vastly complicated phenomenon.

9.1 Since an amoeba is unicellular, it is obvious that the mechanisms involved in its responses to stimuli are contained within its protoplasm. In fact, single muscle cells or nerve fibers can be isolated from a higher animal and used to demonstrate responsiveness of protoplasm. Although such cells are highly coordinated with other cells in the performance of their normal functions in the animal body, it is clear from experiments involving single cells (whether from amoeba or from highly differentiated tissue) that responsiveness is not entirely dependent upon intercellular relations. Rather, it is a fundamental property of protoplasm, as are metabolism, growth, and reproduction. Like these characteristics, it reaches its most pronounced form of expression in highly complex organisms, but it should be remembered that *protoplasm itself is responsive to stimuli*.

Let us analyze the events that occur when protoplasm exhibits the characteristic of responsiveness. If an amoeba is touched lightly with a fine-pointed glass rod or needle, its fluid protoplasm begins moving in a direction away from the point of contact. In the entire sequence of events, three phases are evident: *reception* of the stimulus, *conduction* of the resulting impulse throughout the cell, and *response* on the part of the protoplasm. This series of events also occurs in higher animals, where specialized cells or parts of cells

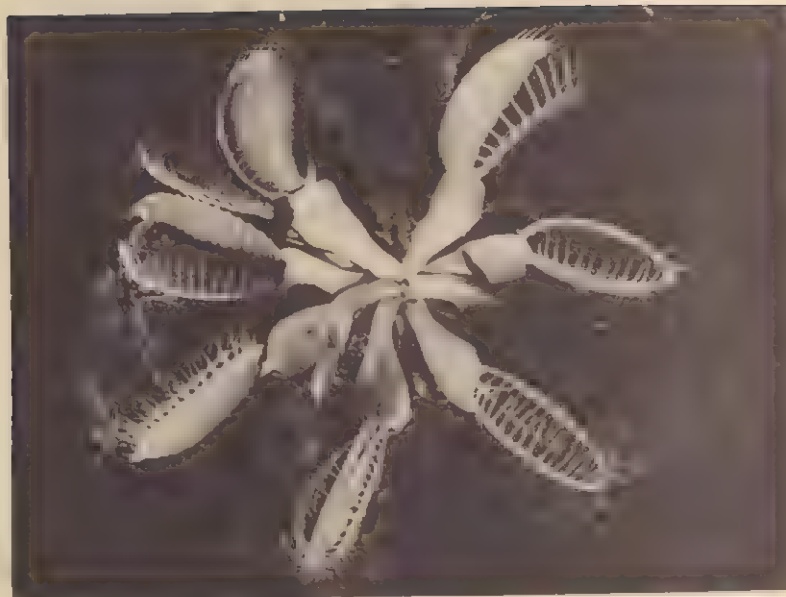


Figure 9.1 *Dionaea*, the Venus fly-trap. This is an insectivorous flowering plant of bright green color, shown here a little larger than natural size. Its leaves ("traps") close suddenly in response to the movement of insects against certain hairs on the internal leaf margins. (Carolina Biological Supply Co.)

serve as receptors, conductors, and effectors in the accomplishment of responsiveness. Since we are accustomed by this time to thinking in terms of histological specialization, we can readily accept and partially understand reception, conduction, and response on that level. However, an amoeba is not equipped with nerves or muscles, and responsiveness must be accounted for on a cytological rather than a histological basis. Actually, biologists do not as yet have a very satisfactory explanation for the events occurring in protoplasmic responsiveness because the physical and chemical factors involved are extremely complex. However, it is clear that individual cells are highly organized (a point which must be emphasized repeatedly in the study and teaching of biology), and some of the same forces that are responsible for metabolism, growth, and reproduction make possible the phenomenon of responsiveness also. In the case of unicellular organisms, the entire surface of the cell is apparently capable of responding to certain stimuli, for example, touch. From the point of contact, it may be assumed that a wave of reactivity spreads throughout the cell, setting in motion forces which determine a response. Some unicellular forms possess specialized organelles that are sensitive to light (for example, the "eyespot" of many unicellular algae), and conduction must of necessity begin there in its effect on the organism. Response in unicellular plants and animals is most readily observed when motility is exhibited. This may be accomplished by means of cilia, flagella, or flowing action of protoplasm (as in amoeba). Regardless of the details involved, any

consideration of protoplasmic responsiveness must take into account the phases of reception, conduction, and response.

Whenever a motile unicellular organism responds to a stimulus in such a way that movement is effected, the response is called a *taxis* (Gr. *taxis*, arrangement). For example, if a jar containing pond water is placed under conditions which allow a moderate amount of light to fall upon it from one side only, there is an accumulation on the lighted side of the jar of any motile algae that may be present. Such response to light is called *positive phototaxis*. In contrast, any amoebas present withdraw from the light and tend to collect toward the darker side of the jar. Hence, they are said to exhibit *negative phototaxis*. Various types of stimuli may be used to demonstrate tactic responses, and studies involving protoplasmic activity of this sort have contributed much to an understanding of animal behavior.*

9.2 Responsiveness in animals Although tactic responses are exhibited by *Amoeba* and other protozoans, animals higher in the scale of complexity than sponges possess more elaborate and coordinated systems which constitute a basis for responsiveness. This is made possible by the differentiation of cells into nervous tissue, whose conspicuous properties are reception of stimuli and conduction of impulses. Muscle and glandular tissues are also products of differentiation, and they are the chief types of effectors in response. In the vertebrates, and especially in mammals, coordination of nervous, muscular, and glandular tissues makes possible a vastly complex system of reception, conduction, and response within the body.

The basic functional unit of responsiveness in the more complex animals is the *reflex arc*, which consists of five basic components: *receptor*, *sensory* (afferent) *pathway*, *modulator*, *motor* (efferent) *pathway*, and *effector*. A specialized receptor, sensitive to a particular stimulus, converts it into an impulse which is passed along a sensory nerve fiber (afferent pathway) to the modulator (brain, spinal cord, or both), where the impulse is interpreted. In turn, the modulator sends impulses over motor nerve fibers (efferent pathway) to effector organs (glands, muscles), thus eliciting a response (Figure 9.2). Hence, a reflex arc is characterized by four interdependent processes: *reception*, *conduction*, *modulation*, and *effect*. Each of these processes is considered separately below.

* The term "taxis" is also applied to movements of multicellular animals in response to stimuli. Many insects, for example, are described as being positively phototactic. Since the behavior of multicellular animals is dependent upon the interaction of many specialized cells, it is doubtful that the same term should be used at all levels of complexity. However, possibly for want of a better term, *taxis* is applied more widely than at the level of protoplasmic responsiveness.

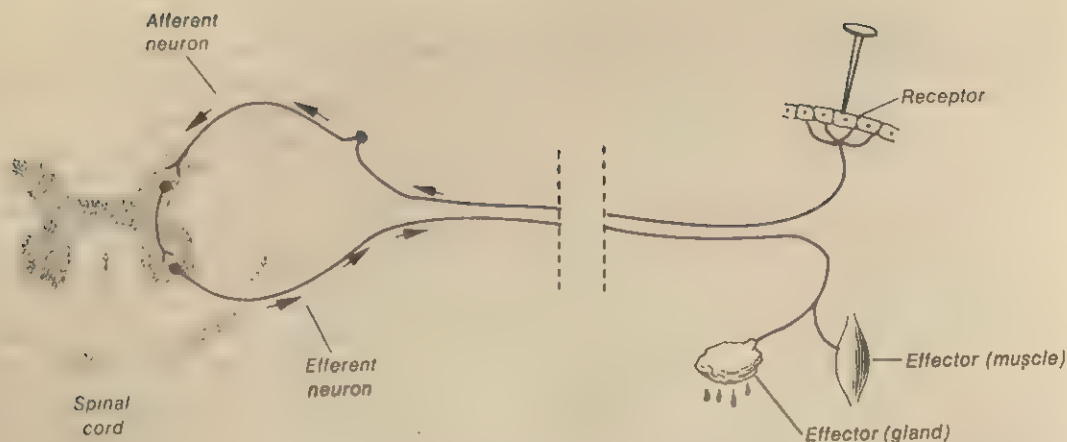


Figure 9.2 Diagram showing a reflex arc in its simplest form as it functions in a vertebrate animal. An impulse originates with a receptor, travels to the modulator through an afferent neuron, and passes out of the modulator through an efferent neuron. An effector structure (muscle or gland) responds to the stimulus. Fibers of the afferent and efferent neurons shown here are greatly reduced in length.

Reception There are many types of stimuli to which animals are responsive. Some of the more common stimuli are changes in light intensities or wave lengths, various lengths of sound waves, temperature changes, pressure changes, and chemical changes. Highly specialized sensory receptors located at various points in the animal body receive these stimuli, and as a consequence, impulses are initiated along afferent pathways. Eventually, these impulses are interpreted in a modulator structure as a "message."

Receptors may be classified from a number of different viewpoints. Those receiving stimuli from the external environment (outside the animal body) are termed *exteroceptors*, while those receiving stimuli from the internal environment (inside the animal body) are termed *interoceptors*. Receptors may also be classified on the basis of the type of stimulation to which they respond, as follows: *photoreceptors* (light), *pressoreceptors* (touch and pain), *chemoreceptors* (chemical changes such as occur in taste and smell), *thermoreceptors* (temperature), and *phonoreceptors* (sound vibrations). From another viewpoint, receptors may be classified as *neurosensory* cells and *epitheliosensory* cells. A neurosensory cell exhibits several branches, or fibers, and the terminal portion of each branch constitutes the receptor. In contrast, epitheliosensory receptors have a cellular identity other than that of a nerve cell. They receive stimuli at

one end while making contact with nerve cell branches at the other. In either case, receptors may be aggregated into clusters to form sense organs. Some of these sense organs, such as eyes and ears, are extremely complicated structures. All of the sensory receptors of invertebrates are of the neurosensory type, whereas vertebrates possess both types. Figure 9.3 illustrates these two types of receptors.

Regardless of type, receptors share the ability to transform stimuli into impulses. The nature of the nerve impulse is discussed below but it should be emphasized at this point that the impulse is evidently generated in the receptor by some electrochemical process which is poorly understood at the present time. Impulses all seem to be of the same basic nature regardless of the type of stimulus or receptor involved. For example, impulses associated with the sense of taste do not seem to be different from those associated with other senses.

Conduction The basic unit of impulse conduction is the *neuron* or *nerve cell*. Neurons are classified as *unipolar*, *bipolar*, and *multipolar* on the basis of the number of fibers leaving the main nerve-cell body (Figure 9.4). The multipolar neuron is the type found to be most abundant in the animal body. It consists of a central body containing the nucleus, several cytoplasmic extensions (*dendrites*), which transmit impulses to the cell body, and a single cytoplasmic extension (*axon*), which transmits impulses away from the cell body (Figure 9.4). In the case of bipolar neurons, there is one axon and one dendrite, while unipolar neurons possess a single axon which divides into two branches, the *central* and *peripheral* processes. In neurons that represent the initial stage of an afferent pathway, the terminal ends of dendrites may either be modified into neurosensory receptors or may establish contact with epitheliosensory receptors. The axons of terminal neurons in an efferent pathway make contact with an effector structure such as a muscle or gland.

The long fibers (axons) of many neurons may be bound together by connective tissue and membranous structures to form a *nerve*. A nerve may be composed entirely of axons of afferent neurons, or those transmitting impulses toward the modulator, in which case the nerve is termed a *sensory nerve*. In contrast, a nerve containing axons of efferent neurons carrying impulses away from the modulator is called a *motor nerve*. Some nerves contain axons from both afferent and efferent neurons and are termed *mixed nerves*.

The precise nature of the nerve impulse generated in the receptor and passed along the nerve cells is still incompletely understood. However, some insight has been gained within recent years. Researchers in this area agree that impulse conduction is an electrochemical phenomenon. The cell membrane of the inactive neuron fiber is polarized, that is, it is positively charged on the outside and

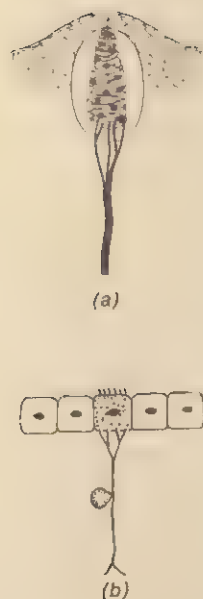
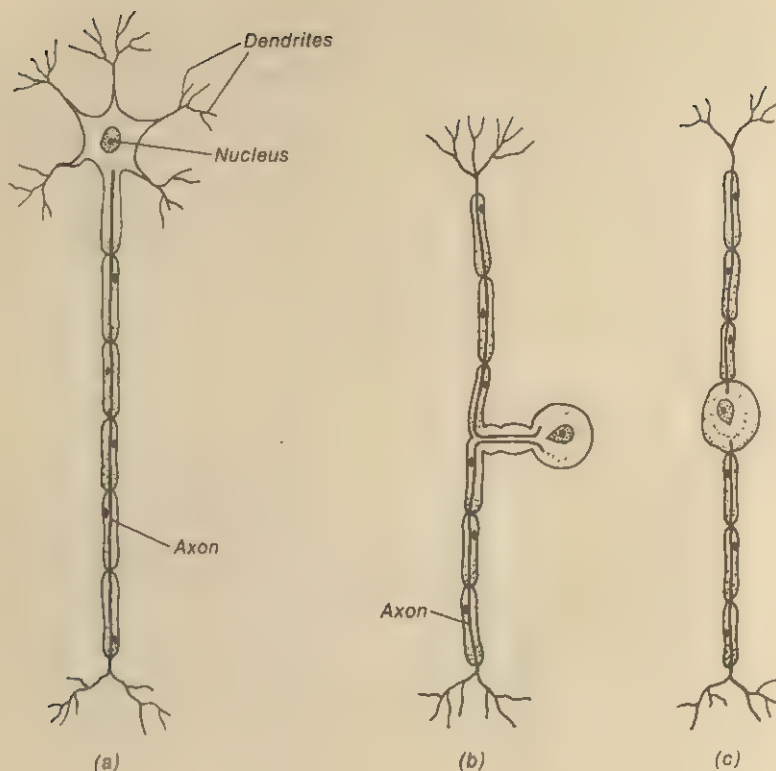


Figure 9.3 A comparison of the two basic types of receptor: (a) neurosensory receptor shown lying within the epidermis of the skin; (b) epitheliosensory cell in contact with a neuron

Figure 9.4 A comparison of the three basic types of neuron: (a) multipolar neuron; (b) unipolar neuron; (c) bipolar neuron



negatively charged on the inside. As an impulse travels along the fiber, the membrane of the fiber becomes depolarized (Figure 9.5). Thus, the action wave or impulse is the result of a depolarization of the fiber membrane. Furthermore, there is general agreement that this polarization of the membrane is due to its selective permeability with regard to certain ions. A number of studies have shown an ionic imbalance on the two sides of the membrane in the inactive neuron. About 90 percent of the charged particles outside the membrane are sodium (Na^+) and chloride (Cl^-) ions, whereas these same ions account for only about 10 percent of the total charged particles inside the membrane. Apparently, there is a relatively high concentration of large negatively charged organic ion radicals on the inside to which the membrane is impermeable. Potassium ions (K^+) also seem to be involved, and in the inactive membrane, they are more highly concentrated on the inside surface. The imbalance of Na^+ and K^+ across the membrane is puzzling, since they are both monovalent, positively charged ions of about the same size.

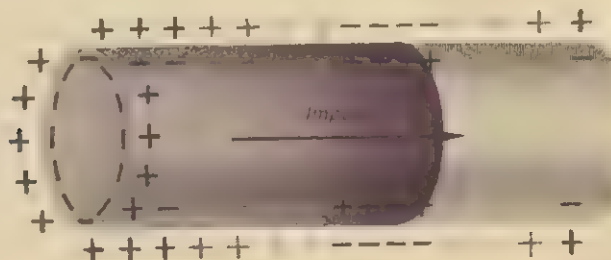
Although there is some disagreement among nerve physiologists

with regard to the nature of the impulse, the following account is widely accepted as a working theory. The membrane of the nerve cell fiber is freely permeated by K^+ but not by Na^+ and the large negatively charged organic ion radicals. Although Na^+ may enter the cell through the membrane, it is not retained; rather, it is "pumped" out by some means. In spite of the permeability of the membrane to K^+ , these ions are held predominantly inside the membrane due to the strong electrical attraction of the large negatively charged radicals. It appears that for every sodium ion held outside the membrane a potassium ion is retained inside the membrane. This results in a net positive charge outside the membrane and a net negative charge inside, thus creating an electrical potential across the membrane. The stimulation of a receptor seems to interfere with the outward transport of sodium ions temporarily, and as a result, they rush through the membrane to the interior of the fiber. This occurs in progressive fashion along the membrane, with the result that an impulse (depolarization wave) passes along the fiber. It is thought that as Na^+ initially rushes to the interior of the fiber the charges are reversed momentarily, but that within a few milliseconds the sodium "pump" is turned on again and the inflow of Na^+ is stopped. At this point, potassium leaks out of the cell, restoring the positive charge to the outside of the membrane. Within a few milliseconds, however, the initial situation is restored, that is, sodium is concentrated outside the membrane and potassium is concentrated inside.

In support of the theory outlined above, it can be demonstrated that an active region of the outer membrane surface is actually negative to inactive regions. Furthermore, it is known that there is a short period of time (a few milliseconds) during which a second impulse will not pass along a particular point of the fiber. This period is called the *refractory period* and it is thought to represent the time that is required by the membrane to reestablish the initial ionic situation.

By way of comparison a receptor bears somewhat the same relationship to a fiber as a "cap" does to a stick of dynamite; it

Figure 9.5 Diagrammatic representation of impulse flow along a nerve fiber. At any given moment, only a fraction of the total fiber membrane is depolarized. Thus, a band of depolarization, represented here by shading, moves along the fiber away from the source of stimulus. Faded charges on either side of the depolarized area represent regions where ionic exchanges are occurring.



responds to a much lower degree of stimulation (called a *threshold stimulus*) than does the fiber itself, and it serves to upset normal polarization in the fiber membrane with which it is connected. Consequently, a wave of membrane disruption spreads along the fiber, each section upsetting the next as the ions come together (Figure 9.5). The fiber quickly recovers its normal polarized condition and is able to transmit another impulse, which explains why receptors can receive separate stimuli at a very rapid rate.

It should be pointed out that the nerve impulse, while bearing certain similarities to the current of electricity which flows along a wire, is not merely an electrical phenomenon. For one thing, a wire only *conducts* a current of energy which must be supplied by the stimulating agent, while the *nerve fiber itself* supplies the energy required by impulse transmission. It thus constitutes an *electrochemical* system rather than a simple *electrical* one. Another difference lies in the relative rates of travel, that of an electrical current along a wire being something over 100,000 miles per second under most conditions. The speed of nervous impulses varies considerably, depending upon (among other factors) size of the fiber and the type of animal involved, but it rarely exceeds one hundred meters per second. It may be as slow as five meters per second, especially in the fibers of certain invertebrates. It is also interesting to note that strength of stimulus has nothing to do with rate of impulse in nerve fibers, just as a powder fuse burns at the same rate whether it is lighted with a spark or with a blowtorch. This principle, which applies to all responsive cellular material of animals, including both nerve and muscle fibers, is termed the *all-or-none law*.

In an afferent pathway, one or more neurons may be involved in transmitting the impulse to the modulator (brain, spinal cord, or both). The point at which the axon of one neuron comes in close contact with the dendrite of another neuron is termed a *synapse*. There is some disagreement as to whether there are anatomical connections between adjacent nerve fiber endings or whether a gap exists. Electronmicrographs strongly indicate, at least in some cases, that the membranes of the two processes make contact with each other. However, the most widely accepted theory holds that transmission across the synapse is dependent upon the presence of a substance called *acetylcholine*, which is apparently secreted by the axon involved. The impulse is thus transmitted to the dendrites of the next neuron in the series (Figure 9.6).

Modulation The nervous system of the complex animal body is generally divided, for convenience, into *central* and *peripheral* parts. The central nervous system consists of the brain and spinal cord, and the peripheral nervous system is composed of all of the neurons

and their cytoplasmic extensions which lie outside the central nervous system. With few exceptions, it is within the central nervous system that modulation occurs. The peripheral system functions in relaying impulses to and from the central system. The spinal cord and brain are composed of aggregations of nervous tissue which constitute centers of modulation. The incoming impulses from afferent pathways may be modified here and transmitted to various points in the body. The nerve cell bodies of motor neurons are located within the central system; thus, impulses which travel outward originate in the brain or spinal cord. In a simple reflex arc, the impulses may simply pass through a chain of three neurons, as shown in Figure 9.2. In other cases, the impulse may be transmitted over nerve tracts or pathways in the cord to various regions of the brain, in which case modulation becomes a highly complex phenomenon.

The nerve cord and brain are composed of complex bundles of nerve fibers called *tracts*, or *pathways*, and dense accumulations of nerve cell bodies called *nuclei*. The larger nuclei are functionally subdivided into *centers*. Some centers control involuntary activity and others control voluntary activity. From a different functional viewpoint, some centers are active in the interpretation and appreciation of incoming sensory impulses from specific localities. Thus a particular sensation appreciated from some particular locality in the body is a function of the modulator (brain) rather than of a specific impulse type. For example, one feels pain in the hand because impulses are channeled to the precise locality in the brain for appreciating pain in this particular region. Figure 9.8 illustrates some of the gross morphological features that vertebrate brains may exhibit. The large groups of nuclei found in vertebrate brains may store informa-



Figure 9.6 Diagram of two neurons in synaptic relationship. An impulse travels along the axon and spreads to the fine terminal branches, where acetylcholine is secreted. The impulse passes from the axon to dendrites of the adjacent neuron, then to the cell body, and from there to the axon.

tion in the function of learning, and in general they coordinate the intricate patterns of behavior characteristic of these complex animals.

In the higher animals, the muscle fiber is the chief type of effector structure. As we emphasized previously, it is a type of cell which is highly contractile, thus making possible the movement of those animals which possess them. A great many complex factors are involved in the contraction of a muscle fiber, but energy derived from the breakdown of ATP to ADP is responsible for the work that is accomplished. Each muscle fiber is caused to contract when an impulse reaches it by way of a motor nerve cell fiber (Figure 9-2); apparently a series of reactions are set in motion by the impulse, the net result of which is a shortening of the fiber. Now the muscle fiber itself is subject to the all-or-none law and contracts to the full extent of which it is capable, but it must be remembered that a great many fibers constitute a muscle. Fibers usually contract in groups, and it depends upon how many groups are activated at one time as to how much total work a given muscle may perform. Hence, the entire muscle is not subject to the all-or-none law; only its individual fibers are.

Another important point regarding muscle contraction involves the principle that it is a one-way process: that is, once having acted, the muscle fibers must be extended back to their original lengthened position. In other words, they work only by contracting, not by extending. In the skeletal muscular system of vertebrates, there are usually *antagonistic* muscles (Figure 9-7) which work oppositely to each other; the contraction of one extends the other, thus putting it into position to contract when it is stimulated by a volley of nerve impulses. Although the muscle fibers of the internal organs and heart are not organized into definite muscles, groups of fibers serve as antagonists to others, and the same effect is realized.

In addition to muscle fibers, there are other types of effectors in multicellular animals. It was mentioned earlier that energy expenditure may take the form of electricity and light in certain organisms. The structures which are associated with such energy release obviously constitute effectors, and it is known that reflex arcs are involved in their action. In all vertebrates and some invertebrates, groups of cells function as glands in the secretion of a particular chemical product. Although some of these are under the influence of nerve impulses, others respond to certain chemical influences such as a high or low concentration of some particular substance present in their environment. Hence, gland cells of the latter sort constitute a *chemical* type of factor in responsiveness, as contrasted to the *electrochemical* nature of the reflex arc. We shall have more to say about these glands in the next section.

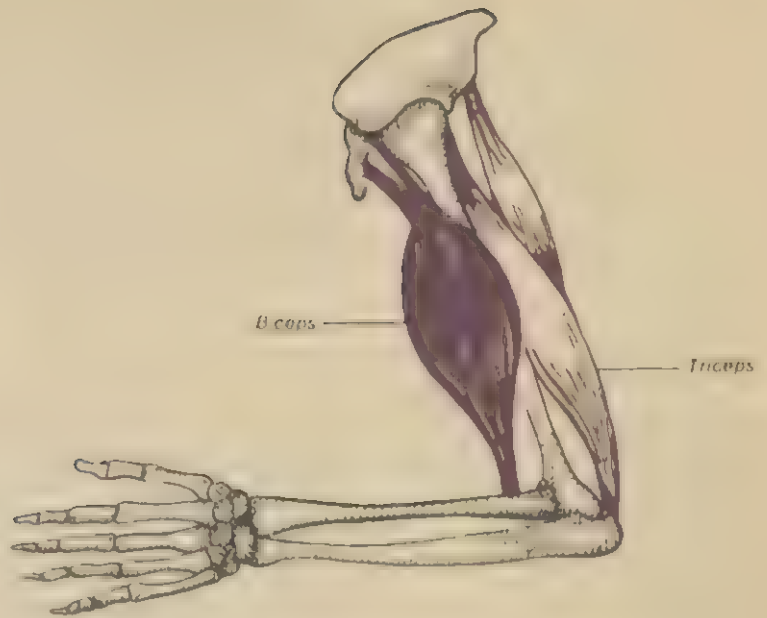


Figure 9.7 Muscular antagonism in the human arm. In its contraction, the biceps pulls the forearm upward, and at the same time the triceps is extended. Contraction of the triceps then pulls the forearm downward and extends the biceps

By way of summary Figure 9.2 represents all of the parts of a typical reflex arc. A stimulus is applied to the outer surface of the body and this causes the sensory receptor (modified end of the peripheral fiber of a unipolar neuron) to fire, sending an impulse along an afferent pathway into the cell body of the neuron. The fiber in this case is located in a spinal nerve, and it travels through one portion of the nerve and enters a dorsal root ganglion where the cell bodies of several unipolar neurons are located. The impulse is then transmitted to the spinal cord (modulator) where it synapses with a connecting or association neuron in the dorsal portion of the cord. The association neuron then synapses with a motor neuron in the ventral portion of the cord, and the impulse is channeled out over an efferent pathway through the spinal nerve which supplies an effector (for example, a muscle or gland).

Actually, the pathway above represents a very simple example of responsiveness in animals. It would be extremely difficult, except under special experimental circumstances, to stimulate only one receptor; furthermore, only one muscle fiber (or even several) would ordinarily have very little effect in initiating a response since muscles are usually composed of many thousands of muscle fibers. When the skin of a vertebrate is touched, for instance, a great number of impulses are initiated. Several of these may travel to effector struc-

tures, while others lead to areas of the brain that are concerned with consciousness. Responsiveness in the higher animals is dependent upon a system of nerve cells, fibers, synapses, and effectors of sufficient complexity as to be almost beyond comprehension. Nevertheless, much is known about certain reflex patterns, and a functional basis for understanding the sum total of responsiveness, or the *behavior* of an animal, has been developed as a result of knowledge gained in regard to the nature of impulse transmission and the reflex arc.

9.3 Behavior of animals We have so far said more about reception and conduction of stimuli than about the responses they produce.

The sum total of all the mechanisms of responsiveness that are operative in a given animal constitutes its behavior. Since no two animals receive exactly the same kinds or amounts of stimuli, there is a great deal of individual variation in the behavior of even two members of the same species. In fact, the same animal exhibits different behavior under differing conditions, and in at least many vertebrates and higher invertebrates, it is frequently difficult to predict exact behavior from a certain set of stimuli.

Theoretically, at least in terms of the reflex arc, a given stimulus should always produce a specific response. In animals such as cnidarians, and in isolated situations among more complex animals, this is usually the case. Behavior can be predicted when a stimulus always produces the same response in a given animal; the organism in such cases is entirely under the influence of its reflexes. For example, if a crystal of carbolic acid is brought into close proximity with the oral end of a hydra, it will invariably contract its body. This type of behavior is termed *unconditioned behavior* because it depends upon a particular kind of synaptic relay called an *unconditioned reflex*. It is not limited merely to those animals that are lowest in the phylogenetic scale. Man exhibits quite a number of such reflexes, for instance, a tap made just below the knee normally causes certain muscles of the leg to contract, thus producing a "kick." Every multicellular animal above the level of sponges possesses a number of such reflexes, most of which function in some way in its protection or well-being. Thus, the unconditioned reflex is probably established in an animal during its embryonic development.

Only in the least complex animals are reflexes completely unconditioned, or as they are sometimes designated, *unlearned*. With an increase in complexity of nervous systems, and in almost direct proportion to such an increase, animals are seen to exhibit the ability for *learning*. Apparently, the capacity for learning is a biological

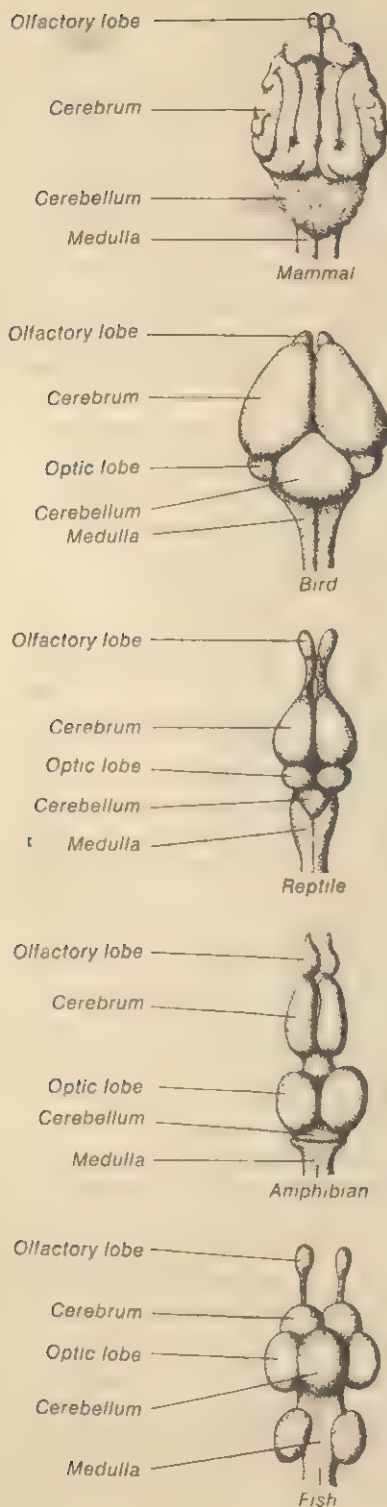


Figure 9.8 The comparative structure of vertebrate brains. They are drawn to the size that they would have if they were all of approximately the same weight. Even with this adjustment, note the difference in size of the cerebrum.

phenomenon which is exhibited only where sufficient reflex pathways exist that the animal is able to utilize some of them in developing responses to stimuli that it was not "born" to make. These new responses are termed *conditioned* or *learned* reflexes.* In most invertebrates, the capacity for learning is quite limited, although animals as low in the scale of complexity as flatworms may be taught to respond to stimuli. Even the lower vertebrates exhibit relatively little adaptability in this respect, although it seems certain that many responses are learned by trial and error on their part. With the increase in relative size of that portion of the brain known as the *cerebrum*, however, animals are seen to learn much more readily (Figure 9.8) If we knew no more than this about the relation between structure and function in nervous systems, we could assume that the cerebrum is directly involved in learning. Actually, experimental evidence has accumulated which shows that although this portion of the brain serves other functions than the facilitation of learned responses, increase in size of the cerebrum (phylogenetically speaking) makes possible the development of more association nerve cells. This, in turn, provides for more reflex pathways, and a greater degree of learning is thus made possible.

Although most animals can learn, which means that their behavior is at least partially determined by conditioned reflexes, the vast majority are governed almost entirely by unconditioned pathways of stimulus and response. Whenever a set of unconditioned responses are coordinated in such a way as to result in a particular act or set of acts directed toward the accomplishment of a specific end, we call such behavior an *instinct*. It is extremely difficult to determine with certainty that all instincts are *purely* innate, especially in higher animals where experience may have suppressed or modified the original inborn set of reflexes involved. There are instances, however, where it becomes clear that some instincts are not affected at all by learning. Females of a group of nonsocial insects known as digger wasps demonstrate this point very well in their behavior. After

* It should be pointed out that there is no actual movement, or switching, of nerve fibers to form new or different synapses in the process of learning. The conditioned reflex is functionally, not structurally, new to the animal. New functional pathways are probably accomplished chemically through an alteration of the thresholds of certain synaptic connections. This, in turn, makes certain pathways more likely to "fire" than others.

she has mated, a female digs a burrow in the ground, and goes off in search of a certain type of caterpillar. Upon locating her prey, she paralyzes it with her sting and carries it to the burrow, within which it is deposited. She then proceeds to lay an egg and to attach it to the outer surface of the caterpillar, whereupon she leaves the burrow, seals it over, and never returns to it. This process may be repeated many times by a given female. Under these conditions, the egg hatches into a larva, which feeds upon the paralyzed caterpillar. Ultimately, it spins a cocoon, undergoes pupation, and develops into an adult wasp. An adult female produced in such a manner ordinarily would never even see its mother, and certainly it receives no instruction from her as to how the reproductive process should be carried on. Nevertheless, as soon as she has mated, the new female will repeat the process exactly as it has been done by thousands of generations of her female ancestors. Clearly, her reproductive behavior is a matter of instinct.

It is apparent, then, that some of the higher invertebrates possess special instincts which make it possible for them to exhibit unusual coordination of activities. This is particularly obvious among social insects such as bees and ants where complex colonies are maintained with a minimum of confusion. Some people actually believe that these animals are very nearly as intelligent as human beings and that in their behavior they demonstrate great learning ability. Although some learning does occur in such forms, it is definitely at a minimum *in determining total patterns of behavior*. By and large, conditioning merely serves the instincts. For example, a honey bee learns how to orient herself in relation to the hive, and she is thus able to travel a considerable distance from it and still find her way back. However, her behavior within and away from the hive is almost wholly instinctive. In using the term "intelligence," most students of behavior prefer to define it in terms of capacity for learning, especially with regard to the solving of problems. In the light of this concept, social insects are still among the most intelligent of invertebrate animals, but they are, nevertheless, quite limited. Only in the higher vertebrates do we find any great degree of real intelligence, and even there instincts are involved in behavior to a considerable degree.

As we have observed, learning seems to be largely a matter of developing conditioned reflexes. When a group of such reflexes become coordinated in such a way as to determine a given act or set of acts in behavior, a *habit* is formed. In other words, a habit is a particular learned response which is made to a given stimulus or groups of stimuli. Thus, at least within certain limits, a habit bears much the same relationship to conditioned reflexes as an instinct

does to unconditioned ones. Although it is true that conditioning and response may occur without habit formation, just as isolated responses of an unconditioned nature do not necessarily constitute instincts, most learning does eventually contribute to certain patterns of behavior that can be called habits. Perhaps this statement could be justly challenged were it not for our realization that many habits are developed in the higher animal, and particularly in the human, which are not always recognized as such. A moment of reflection should produce the realization that most of our actions come under this definition. We grow so accustomed to doing certain things that we often assume that they are accomplished instinctively. Actually, once a habit is formed in the human nervous system, it usually may be performed with a minimum of conscious effort on the part of the individual. The many separate acts involved in walking, speaking, driving an automobile, and so on, had to be learned at some time. Metaphorically speaking, habits are nature's provision for freeing the conscious mind of responsibility for most acts of behavior that an individual is obliged to perform.

Thus far, we have only considered behavior which results in some way from sensory stimuli. It should be pointed out that, at least in the higher animals, activity may be initiated within the nervous system itself. For example, a person may decide to contract the biceps muscle of his arm, or to kick a ball. The primary signal for initiating such action arises somewhere within the nervous system itself. Now this is not to say that there was no *motivation*, or basic reason for the action, but it certainly did not come about directly as a result of external stimulation. Whatever stimulus may have been provided arose within the individual's own conscious mind. As a matter of fact, the ability of the higher animal, and particularly the human, to manipulate ideas is responsible for a great deal of the total behavior exhibited. Other abilities, including memory and imagination, also play an important part in behavior at this level of intelligence.

We have already mentioned that in the higher animals behavior is affected by glandular secretions and other chemical influences within the body. In the vertebrates and in certain invertebrates, that group of secretory organs known as the *endocrine glands* are perhaps more directly involved in behavior than are any tissues other than the nerve cells themselves. These glands are distinguished by the ability of their cells to secrete *hormones*, which are chemical substances that are taken up by the bloodstream and carried to some part of the body where they initiate a specific response. Some endocrine glands produce only one hormone while others may produce several. The major endocrine structures in man are shown in Figure 9.9.

Hormones are highly specific in their action; that is, they are limited in their effects to those cells which are responsive to their particular chemical influences. For instance, a hormone called *secretin* is produced in the cells that line the internal surface of the duodenum when hydrochloric acid from the stomach comes into

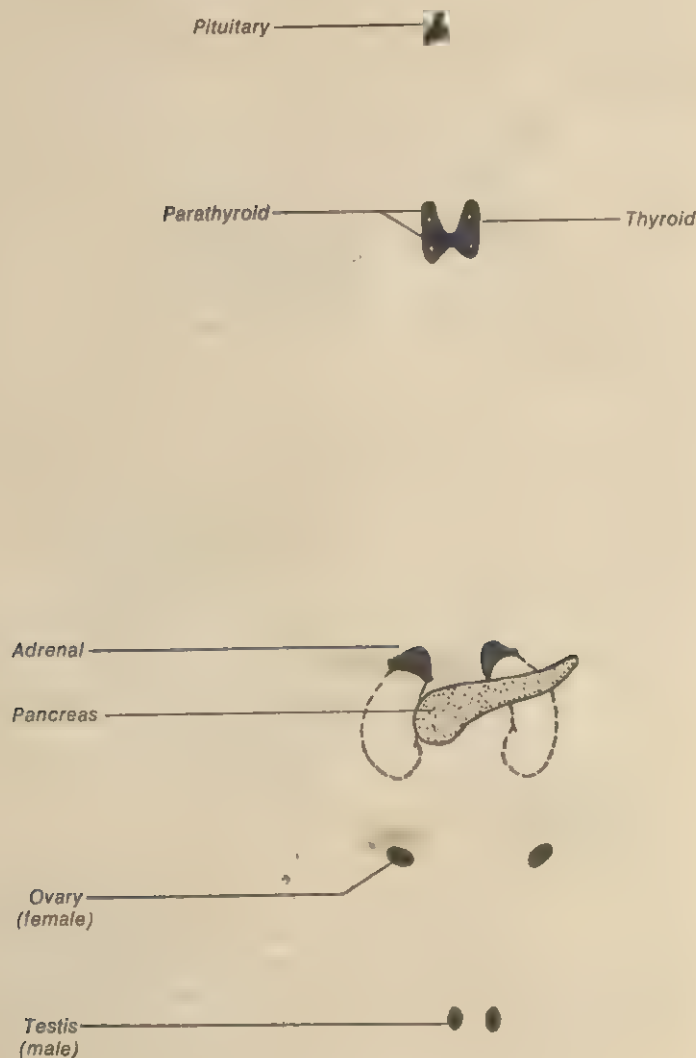


Figure 9.9 The major human endocrine glands. For purposes of representation, both ovaries and testes are shown as they would appear in the female and male, respectively.

contact with them. This hormone passes into the bloodstream and is carried throughout the body; but it apparently exerts no influence on body cells generally. Its specific "targets" are the cells of the pancreas which secrete pancreatic juice. These, in turn, are stimulated by action of the hormone, and their secretory product is carried directly to the duodenum by the pancreatic duct (Figure 6.13). By virtue of this mechanism those enzymes which are functional at this stage of digestion are present at exactly the right time.

It might seem at first thought that such hormonal action as this has little to do with behavior, but it is actually a very important aspect of it. Stimulus and response are certainly involved, and the total behavior of the individual is very definitely affected. In fact, proper hormonal balance is so necessary to normal behavior in the human, for example, that a slight malfunction of an endocrine gland may exert profound effects upon the individual. As in the case of so many other mechanisms that contribute to behavior, we take normal hormonal balance so much for granted that it becomes difficult to realize how important these secretions really are. Some of the more important hormones and their specific activities within the human body are presented in Table 9.1.

The principle of homeostasis is beautifully illustrated by many responsive mechanisms which operate within the complex animal body. We have already called attention (Section 5.3) to the homeostatic nature of the temperature-regulating center; in addition, many other neural mechanisms function in a self-regulating manner. For example, the rate of breathing in the vertebrates is under the influence of certain chemoreceptors located in the aorta. These receptors are extremely sensitive to an increase of carbon dioxide in the blood; if CO_2 concentration is increased by only a small percentage, the receptors are stimulated and send impulses to centers of the brain which control the muscles used in breathing. As a result, the rhythm of inhalation and exhalation is quickened. By this means, elimination of CO_2 is hastened, and its concentration in the blood stream falls. At this point, the chemoreceptors cease to relay impulses to the brain, and the pace of breathing is slowed. Thus CO_2 regulates its own elimination through a homeostatic mechanism. Again, hormonal balance within the complex animal body is largely homeostatic. For example, a human gonadotropic hormone (see Table 9.1) produced in the pituitary influences the production of hormones in the female ovary. These hormones, in turn, influence the pituitary in such a way that production of the gonadotropic hormone ceases. At this point, the ovary is no longer stimulated to produce its hormones, and their concentration within the blood stream falls markedly. After the inhibitory effect of the ovarian hormones is re-

Table 9.1 *Major human endocrine tissues and hormones*

Gland or tissue	Hormones	Major function of hormone
Anterior lobe of pituitary	Growth-promoting Thyrotropic Gonadotropic Lactogenic	Stimulates growth Stimulates thyroid gland Stimulates gonads Stimulates mammary glands
Posterior lobe of pituitary	Pitressin Pitocin	Controls blood pressure Stimulates uterine contraction
Thyroid Parathyroid	Antidiuretic Thyroxin Parathormone	Controls urine concentration Stimulates rate of metabolism Controls phosphorus and calcium concentrations in body fluids
Adrenal cortex	Cortisone and related hormones	Control sodium concentration, carbohydrate metabolism; various other functions
Adrenal medulla	Epinephrine (adrenalin)	Various "emergency" effects on blood, muscle, temperature
Testis	Testosterone and related hormones	Influence development of sex organs and male characteristics
Ovary (follicle)	Estrogenic hormones	Influence development of sex organs and female characteristics
Ovary (corpus luteum)	Progesterone	Influences menstrual cycle, prepares uterus for pregnancy, maintains pregnancy
Placenta (temporary)	Estrogens and progesterone	Function in the maintenance of pregnancy
Pancreas (islets of Langerhans)	Insulin	Influences cellular absorption of carbohydrates, regulates fat storage
Duodenal mucosa	Secretin	Stimulates nonendocrine portion of pancreas

moved, the pituitary commences again to produce the gonadotropic hormone, and the cycle of events is repeated. The entire rise-and-fall pattern is reflected in the female by the periodic release of ova and by the menstrual cycle.

9.4
Responsiveness
in plants
and their behavior

Perhaps the majority of people are not aware that plants exhibit any sort of activity that might be called "behavior." Indeed, there is a fundamental difference between most plants and animals in this respect, but it should be remembered that behavior is the sum total of the responses to stimuli which an organism is capable of making. Since plant cells contain protoplasm just as animal cells do, it is reasonable to suppose that the fundamental capacity which protoplasm shows for responsiveness should manifest itself in some way.

It is true that plants do not exhibit nervous or muscular tissues as animals do, nor are there any plant cells that even remotely approach these in their respective capacities for conduction and contraction. As a result, behavior is much less marked in plants than in animals. In general, reception, conduction, and response are limited to the protoplasm of plant cells themselves. In a very few forms among the higher plants, however, there is a type of coordinated behavior which resembles that of animals to a degree. A flowering plant, the Venus fly-trap (Figure 9.1), bears certain leaves whose marginal hairs are sensitive to touch. Movement of an insect upon the inner surface of the leaf is a sufficient stimulus to bring about the closing response. Leaves of the sensitive plant, *Mimosa* (Figure 9.10), respond very quickly to touch by drooping as though they had become wilted. At first appearance, it is tempting to postulate the existence of nervous tissue or something like it in these plants, but investigation has shown that in all such cases, there are mechanisms whereby turgor pressure is greatly lowered in certain cells. In *Mimosa*, for example, there are cell groups at the base of each leaf stalk and at the bases of the individual leaflets. The cells making up these groups are extremely thin-walled and lose water rapidly when the leaf is shaken. The result is that each plant part bends when its supporting cell group loses turgidity.

Most plant behavior is influenced by the production of *plant hormones* which, like animal hormones, may be produced in one part of the plant and transported to another part, where specific effects are produced. Of the several types of hormones recognized by plant physiologists, the *auxins*, a group of substances that affect growth, have been studied most extensively. Although it is known that different auxins exist, it appears that *indole-3-acetic acid* is the principal one produced by plant cells. The formula for this substance

Figure 9.10 *Mimosa, the sensitive plant.*
(a) Plant whose leaves are in natural position; (b) the same plant after leaves have been touched. (General Biological Supply House, Inc.)



is known, and it has been used extensively in experimental work.

Wherever auxins produce their effects, it seems that they influence cellular elongation. In general, the degree to which a cell elongates is proportional to the amount of auxin present; however, there are many exceptions to this statement because tissues of different plant organs do not all respond similarly to given concentrations of auxin. The production of auxin occurs principally in meristematic cells at the tips of aerial shoots such as stems, young leaves, and flower buds. It appears to be produced only in extremely small amounts at root tips. From these sites of production, it may pass by diffusion to older cells.

A number of experiments have been devised to demonstrate the effects of auxins. One of the simplest to perform involves cutting off the tip of a germinating oat seedling* and observing the effect. It is seen that when this is accomplished, the remainder of the shoot virtually stops growing. If the tip of another shoot is placed on this stump, however, growth immediately resumes at a normal rate. If a block of agar (a material used in culturing bacteria) is placed beneath a cut tip for an hour or two and is then laid upon the stump of a shoot, growth also resumes.† Apparently, auxins have moved into

* Auxins were first studied in the oat (*Avena sativa*), whose germinating shoot lends itself especially well to such growth studies. Actually, this experiment could be conducted on any number of higher plants.

† As a control, an agar block which has not been in contact with a tip may be placed upon the stump of a shoot. Under these conditions, there is no resumption of normal growth.

the agar block from the tip, and will in turn move from the block to the stump, where they produce the characteristic effects. Again, if an auxin-laden block is placed on *one half* of the stump, growth occurs only on that side. These experiments are illustrated in Figure 9.11.

Experiments such as these have led plant physiologists to the conclusion that auxins are responsible for many growth phenomena in plants and that these phenomena are influenced in a number of ways. One of the most important environmental factors to which auxins are sensitive is light. If a potted plant is set on a window sill in such a way as to receive light chiefly from one direction, it grows toward the source of light (Figure 9.12). A growth response of this sort is called a *tropism* (Gr. *trope*, a turning), and since the factor initiating the response in this case is light, it is termed *phototropism*. The influence of light is not always such as to cause a plant organ to grow in the direction of its source; it may grow away from it. Hence, phototropism (as well as other tropisms) may be *positive* or *negative*. The growth of a plant stem toward light is, of course, an example of positive phototropism. Evidence has accumulated showing that, under conditions where a stem receives light principally from one direction, there is a migration of auxins from the lighted side of the tip to the shaded side (Figure 9.13). This means that cells of the stem

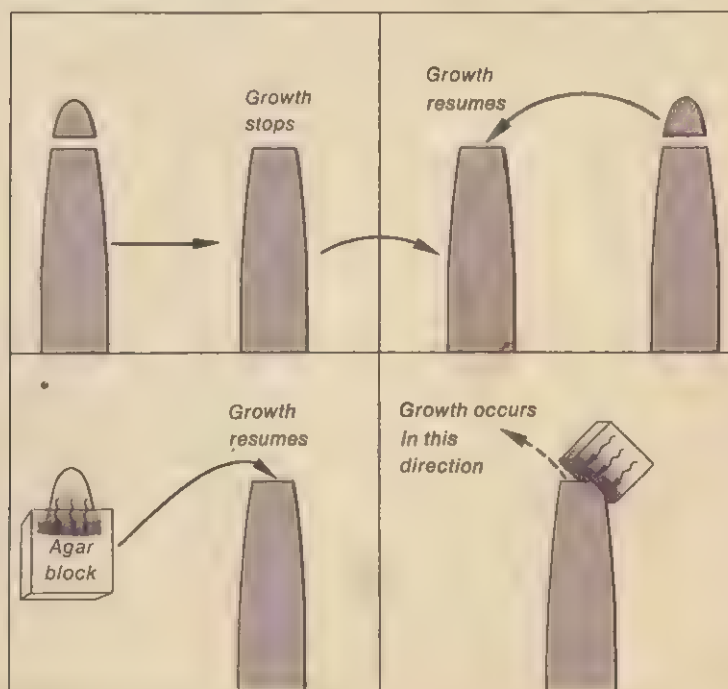


Figure 9.11 Various growth effects exhibited by oat seedlings under different experimental conditions. See text for amplification.

Figure 9.12 A demonstration of positive phototropism. These two *Coleus* plants were potted when they were quite small and were allowed to remain on a window sill for several days. The left-hand plant was turned 180 degrees daily, while the right-hand plant was not disturbed.



on the shaded side receive more auxins and thus exhibit a greater degree of elongation, the net result of which is a bending toward the light. It appears that there is also a certain amount of auxin destruction or inactivation by light. This is indicated in a negative way by the tendency of a shoot to elongate greatly when grown in the dark.

Another important environmental factor that influences growth through an effect upon auxins is gravity. In response to this force, a plant organ may exhibit positive or negative *geotropism*. In a germinating seedling, the root is positively geotropic (tending to grow toward the center of the earth), and the shoot is negatively geotropic (Figure 9.14a). If growth of the embryonic plant is allowed to proceed sufficiently far that these responses become evident, and then the plant is turned so that both root and shoot are horizontally rather than vertically oriented (Figure 9.14b), within a few hours these organs begin to bend in their respective responses to gravity (Figure 9.14c). The explanation here seems to be that in the shoot auxins gravitate to the lower side, as a result of which an elongation of cells occurs in that region. Hence, there will be a turning upward of the stem and leaves. In the root, there is also an accumulation of auxins on the lower side, but instead of being stimulated by the heavier concentration, root cells are so constituted that elongation is inhibited by amounts of auxin that are sufficient to stimulate cellular growth in the stem. Within certain limits, therefore, auxins produce opposite effects in the young root and shoot. Actually, there are many important factors involved here, and secondary roots or stems may respond to gravity in an entirely different manner than that described. Many roots, for example, grow horizontally within the soil.

Nevertheless, early growth in most plants is readily explained on the basis of auxin influence on elongation of cells as described above.

Many other types of tropic responses besides those discussed here are operative in plant behavior, but perhaps these examples are sufficient to show that definite mechanisms have been discovered which account for growth phenomena and other activities exhibited by plants. A consideration of these as well as that of such interesting topics as changes in the colors of leaves, leaf fall, and ecological



Figure 9.13 Auxin destruction and migration under the influence of light resulting in positive phototropism. Cells on the shaded side of the stem tip elongate more rapidly than do those on the illuminated side, causing a bending toward the light source.

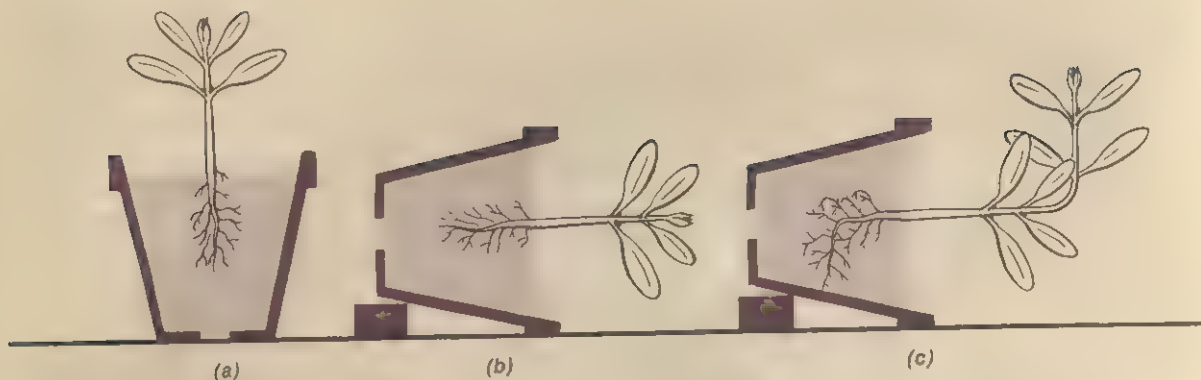


Figure 9.14 Positive and negative geotropism. (a) Potted seedling in normal position of growth (b) The same plant turned 90 degrees (c) The responses shown by root and shoot to the influence of gravity.

adaptation must be left to those specialized fields of botany whose particular interest they are.

**Philosophical considerations
associated
with responsiveness**

9.5 Perhaps we are justified by this time in considering the impact that certain biological principles have had upon the thinking of man with regard to problems of ultimate reality. Although Chapter 12 is devoted in part to such considerations, it seems appropriate at this point to suggest that many of the principles that biologists have clarified pertaining to the general phenomenon of responsiveness have an extremely important bearing upon questions which are often considered to be philosophical, not biological, in nature.

Anthropomorphism One important change in thinking which has come about as a result of an improved knowledge of responsiveness and its mechanisms is in regard to a long-standing (and still existent) tendency of man to interpret nature *anthropomorphically* (Gr. *anthropos*, man + *morphos*, form). This rather long word simply represents a viewpoint that interprets the actions of any given organism or the condition of an object as arising from an intelligence similar to that of man. For example, if a child bumps into a door, he may blame the door for having been in his way, and "punish" it with a kick. Of course, the door is in no way responsible for the incident. On a somewhat higher level, the bending of a plant toward light may be interpreted (and often is) according to an anthropomorphic view. According to such a concept, it might be said that the plant "likes" the light because it thrives under its influence and thus "tries" to grow toward it. Now biologists have absolutely no reason to suspect

that plants are equipped with the capacity for awareness, and we feel quite safe in saying that the particular plant under consideration does not like or dislike anything; its actions are simply the result of auxin influence. In other words, plants do not *try* to do things, but they *do act*.

As long as we are dealing with nonliving objects and with plants whose lack of consciousness may readily be accepted, we have little difficulty with anthropomorphism, but where, in the animal kingdom, do we stop dealing with completely mechanistic, or determined, behavior and enter into a realm of such complexity that we are obliged to ascribe awareness and purpose? Actually, this becomes quite a problem, and we shall consider some of its more important ramifications later. For the time being, it may simply be mentioned that good reason exists for believing that the least complex animals whose behavior is entirely dependent upon unconditioned reflexes are no more "aware" than are plants. We are obliged to view them as machines, albeit extremely complex ones, and their behavior is entirely explicable on the basis of stimulus-response mechanisms. Apparently, the capacity for awareness is an emergent quality which comes into being in those animals whose nervous systems are sufficiently complex as to allow for some degree of learning, but just where it begins is a very difficult matter to determine. Certainly we feel justified in ascribing it to vertebrates and to some of the more complex invertebrates. Nevertheless, it is possible to interpret behavior on this higher level anthropomorphically. For example, a household pet may displease us by some action, and whether it obeyed an instinct or forgot a habit does not really matter much if we ascribe to it a degree of guilt or responsibility which is only applicable to human beings.

Free will and determination Although it should be evident that behavior on the part of organisms other than man is not justly subject to consideration in terms of human values, to what extent is one person justified in evaluating the actions of another? This problem, which has been one of considerable importance in all areas of human affairs, including such widely divergent fields as religion and political science, is fundamentally a biological one. Basically, there are two views of man's behavior, namely, the concepts of *free will* and *determination*.

According to the deterministic viewpoint, man is simply the most complex expression of a material universe, where every effect is preceded by a cause. That causes may not be known or understood in no way violates the principle, and since determination is accepted as a way of investigation in all the sciences, human behavior should not constitute an exception to the cause-and-effect principle. Fur-

thermore, since a great many aspects of man's behavior have been explained deterministically (for example, the reflex arc), it may be assumed that total behavior is thus controlled. Hence, according to this viewpoint, man is bound by his instincts, conditioned reflexes, and hormonal secretions as any other animal, and since an individual cannot act differently than he does, he should not be held morally accountable for his actions. What might seem to be a free choice on his part is actually influenced by past experience and instinct. Determination is not to be confused with *fatalism*, however (Fatalism holds that all events are fixed or determined in terms of a predestined cosmic pattern and that human efforts cannot alter them.) It only says that a "choice" between alternatives is determined according to factors that are fundamentally biological ones.

In its literal form, the concept of free will holds that man's actions are *not* biologically determined in the final analysis, but that he has within himself the power to act independently of causative factors. Thus, he is a "free moral agent" and is subject to judgment for his choices between the good and the bad. In its modern expression, this viewpoint concedes that man is not completely free, since many deterministic factors must of necessity be recognized. Furthermore, freedom may be greater in one individual than in another. However, man as an organism is capable of rising above the forces that restrict him, and he has at least some power to make choices.

The significance of the difference in viewpoint between free will and determination may not be immediately apparent to most people because there is a human tendency to suppose that a given person enjoys considerable freedom to make choices. Let us consider a case in point. Suppose a person is taking a walk and comes to a fork in the road. There is no particular reason for him to choose either of the two branches, but he nevertheless makes a decision anyhow. Even though this decision may seem quite arbitrary to him, there are factors of past experience, of imagination, and of his subconscious mind that influence whatever conclusion he reaches. These are all biologically determined by conditioned reflexes, and without knowing it, he may never have really had a choice at all! Of course, he *could* have decided differently, but had he done so, this choice would also have been determined. If this line of reasoning seems to be sheer nonsense, it should be remembered that the question of the freedom of human will has troubled the minds of mankind's best thinkers for many centuries and that it has extremely serious implications for man and his place in nature.

Actually, there are serious difficulties in both concepts. For one thing, these terms are misleading, and much of the difficulty can be eliminated by stating the problem in different terms. Determination

simply means *causation*, which is more easily understood in scientific terms. For example, it is easy to confuse *determination* with *compulsion*, whereas causation simply means cause-and-effect. On the other hand, freedom is simply the opposite of compulsion, and is *not* the same thing as the opposite of causation, which is chance. Thus, to contrast determination and freedom as either-or explanations of human behavior is like defining oranges as the negative of apples.

Within this new framework of thought, then, an act may be both free and determined. For example, the person who decides upon one fork of a road does so for causes either known or unknown to him and the act is thus a determined (caused) one. Nevertheless, the act was not a compulsory one; it was brought about through his own determination, not that of another person. Therefore, it involved freedom of the will (*his* will, not someone else's). However, the observation that determination has often been confused with compulsion and that freedom of the will has been wrongly cast as the opposite of causation does not solve all of the problems. The question of just how free human beings really are continues to have a very important bearing upon many problems which are constantly before society. For this reason, freedom of the will is a very important aspect of responsiveness at the level of human behavior, and is therefore of considerable interest to biology.

9.6 Responsiveness, or the capacity to respond to stimuli, is a characteristic of living systems. At all levels of organization, three phases of responsiveness are evident: reception, conduction, and response. In animals, the major portion of responsiveness is a function of nervous tissue, where the fundamental responsive unit is the neuron, or nerve cell. Neurons are associated together in reflex arcs, which function in the coordination of four processes: reception, conduction, modulation and effect. Muscular tissue plays an important role in the last process. In the complex animal body, these processes achieve a high degree of coordination. For purposes of distinction, two types of reflexes are recognized: those which are conditioned through learning, and those which are unconditioned, or inborn. Responsiveness in the complex animal body also involves hormones, or internal secretions.

Plant responsiveness is fundamentally different to that of animals, inasmuch as no tissues corresponding to nervous and muscular tissues are involved. Rather, most plant behavior is influenced by the production of auxins and other plant hormones. These exert their major effects upon growth processes in the plant, although other processes, such as flowering, are also affected.

Several questions of a philosophical nature are raised by the consideration of responsiveness. We have introduced the problem of anthropomorphism and the apparent conflict of freedom and determination. A discussion of such issues implies that biology may legitimately become involved in philosophical problems which bear upon its materials and methods.

Questions

1 Is responsiveness an exclusive characteristic of living systems? Explain.

2 Describe the structure and function of a typical reflex arc. With regard to any given portion of a nerve fiber, what are the forces involved in impulse transmission? What is the all-or-none "law"?

3 What is the principal means through which plants exhibit behavior?

4 Compare the honeybee and the dog with regard to intelligence, as we have defined the term.

5 What conclusions can be drawn from the experiments involving oat seedlings and agar blocks?

6 There seems to be little doubt that many aptitudes and other differences in intelligence among human beings are influenced by heredity. Postulate a mechanism whereby genes might affect the development of intelligence.

7 For years, it has been argued (mostly by people outside the field of biology) whether heredity or environment is more important in human behavior. Consider this statement from a distinguished geneticist, Charlotte Auerbach: "To the geneticist, questions like 'Is criminality inherited? Is cancer a hereditary disease? Is intelligence the result of education?' make no sense. They presuppose an antithesis which he knows to be wrong, the antithesis between heredity and environment. . . ." [*The Science of Genetics* (New York: Harper & Row, Publishers, 1961)]. Why do such questions make no sense to a geneticist?

8 The growth of a plant stem is influenced (among other factors) by two environmental factors, light and gravity. Devise an experiment which would test the relative effects of these two factors on the direction of stem growth in a bean plant. Be sure to provide adequate controls.

9 Galston (see reference below) discusses agricultural applications of several natural and synthetic plant hormones. Read pages 71-88 in his book and make a list of those he presents.

10 Contrast the philosophies of freedom and determination. How else might the problem of freedom of the human will be stated? Do you feel that man is a free moral agent?

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University of California Associates "The Freedom of the Will," in *Readings in Philosophical Analysis*, eds. H. Feigl and W. Sellars. New York: Appleton-Century-Crofts, 1949. For the student who wishes to read further and more deeply concerning free will and determination, this excellent discussion of these subjects should prove very enlightening.

Adaptation

We have emphasized those characteristics of living forms which are operative in the individual organism. As a matter of fact, metabolism, growth, reproduction, and responsiveness are fundamental characteristics of the cell which find their highest and most closely coordinated expressions in the organism as a whole. Although the process of adaptation very definitely has its roots in protoplasmic mechanisms, it is a term which applies fundamentally to *groups* of organisms—populations, species, and complex aggregations. Of necessity, then, we must consider adaptation in terms of organismic interrelations rather than in terms of individual organisms, as we have largely done to this point. Thus, we shall see that characteristics of the living world emerge at this more complex level, just as those levels constituted by macromolecular systems, cells, tissues, organs, organ systems and organisms each exhibit emergent qualities which do not appear at levels below them.

In studying the biology of groups of organisms, two basic factors must be considered. The first of these is the relationship of organisms in *space* (not *outer* space—we are talking about the space which exists at any given moment on earth) and the second is the relationship of organisms in *time*. This distinction is sufficiently important that we shall devote separate chapters to each factor. For this reason, our present chapter is essentially concerned with ecology, while our next chapter is to be concerned with the subject of evolution.

- 10.1** The term adaptation is sometimes used to describe short-term changes which are actually a form of responsiveness. We often say that man is very adaptable to climatic conditions, for instance, since he can adjust from a warm climate to a very cold one. A more clear-cut example of responsive "adaptation" is seen in the case of less complex organisms, such as protozoa, where certain chemical substances may be added to their aqueous environment by degrees until concentrations are reached that would have killed them if such a quantity of chemical were added all at one time. Evidently, such adjustment is possible through chemical and physical changes in the protoplasm, whose capacity for such adjustment is, of course, limited. However, the very occurrence of such adjustments illustrates the tremendous versatility of protoplasm in responding to environmental changes, and as a type of responsiveness, it is of considerable biological significance. All organisms exhibit the capacity for at least some versatility in this regard.

However, this is not what is meant by adaptation. *This term describes the characteristic of living forms to develop, over a period of time, certain structural and functional features which enable them to survive and reproduce within the limits of a particular environment.*

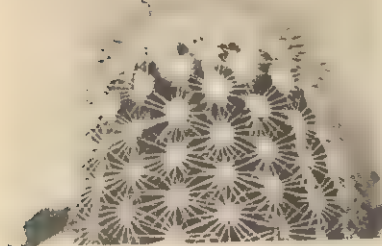


Figure 10.1 Close-up view of a small cactus, showing clusters of spines (modified leaves). Notice their contrast against the darker (green) stem, which is the photosynthetic organ in cacti. How are these leaves and stems related to the adaptation of cacti to their environments?

Hence, when a biologist says that adaptation is a characteristic of living forms, he has in mind a *process*, and one that has gone on throughout past ages, the result of which is the variety of present-day organisms. However, any structural or functional feature of an organism that has been developed by this process may be called an *adaptation*, and so the same term is at once used to describe an overall process in nature and any given result of that process. For example, the stem and leaves of a cactus plant (Figure 10.1) constitute adaptations to a physical environment whose nature is such that plants with typical stems and leaves would be at an extreme disadvantage. The leaves of cactus are greatly modified as spines, and these have very little surface area from which water might evaporate. Actually, they are of little use to the plant except that they prevent desert animals from eating it for the water that it contains. Reduction of exposed surface and loss of photosynthetic ability by these modified leaves have been accompanied in the overall modification of the plant by an emphasis on the stem as a photosynthetic organ. These structural adaptations (spines, photosynthetic stem, and so on) relate the plant to its environment, but they developed over time by the overall process.

10.2 Types of adaptations

In general, any characteristics exhibited by an organism which are of benefit to it in relation to a given environment are primarily either *structural* or *functional* in nature. Structural adaptations are the more obvious, and it would be difficult for even an amateur biologist to miss the direct connection between the morphological features of almost any organism and its environment. We have already called attention to the spines and stems of cacti; these plants exhibit many other structures which make it possible for them to exist successfully where most other plants cannot. To cite another specific example of structural adaptations in plants, many flowers are so constituted as to attract insects which transport pollen from one to another, thus ensuring cross-pollination in the species. In the animal kingdom, structural adaptations are perhaps even more obvious. If one examines the beaks and feet of birds, a direct relationship can be seen between form in these structures and the life habits of the birds. Thus, a duck has webbed feet, and a hawk has grasping claws. In each case, it is not difficult to determine that these adaptations are representative of different modes of existence. It is most instructive to study the mouth parts of different insects, comparing them according to structure. One is thus able to determine rather accurately, without any previous knowledge, to just what type of environment a given insect is related. There are animals whose protective color-

tion or body form is of definite advantage to them; the striped coat of a tiger, for instance, makes it possible for this animal to move through vegetation in search of prey without being readily detected. Conversely, animals frequently exhibit camouflage patterns which conceal them from predators (Figure 10.2). An almost infinite number of examples might be cited, but perhaps these will serve to emphasize the obvious phenomenon of structural adaptation.

Although functional adaptations are perhaps less obvious than structural ones, they also reflect the capacity of an animal or plant to survive and reproduce within the limits of its environment. Bacteria, for example, are capable of producing digestive enzymes that pass out into the medium around them. As a result, food materials in the medium may be dissolved and thus made available to bacterial populations by passing into their cells. Termites, which are insects, possess the rare ability of subsisting upon a diet of wood by virtue of the fact that protozoa in their digestive tracts produce enzymes that hydrolyze cellulose into utilizable sugars. In the vertebrate body, the vastly complex and coordinated enzyme system of the gastrointestinal tract is the result of many adaptations to various food types. These are, of course, only a few of the many functional, or physiological, adaptations that might be cited.

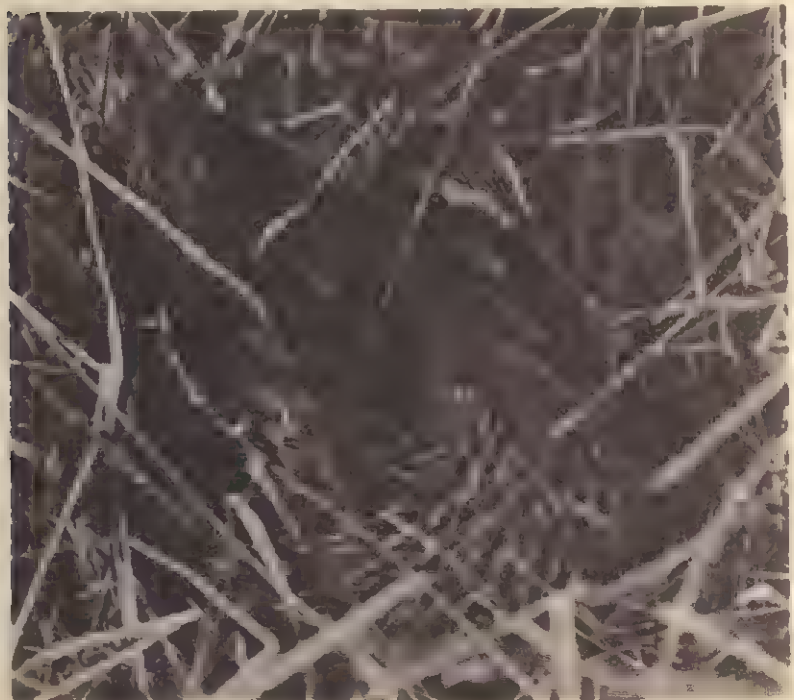


Figure 10.2 *Hen mallard on nest. Notice how her markings blend with the immediate surroundings, providing a protective camouflage. (George Purvis, from Arkansas Game and Fish Commission.)*

Actually, it is impossible to separate structure completely from function in considering a given adaptation, and the distinction made between these two types is merely one of convenience for the sake of discussion. Many adaptations, both structural and functional, work so closely in relating an organism to its environment that the entire phenomenon must be analyzed from the viewpoint of overall behavior, not as a single adaptation. For instance, the courting behavior of many male animals is quite elaborate, possibly consisting of several gestures and acts carried out in a definite sequence. Such behavior is doubtless adaptive for a given animal and plays an important part in the process of reproduction. One can hardly consider courting behavior as a single adaptation; a great many factors, some structural and others functional, make their contribution. There are hormones, unconditioned reflexes, and various effector structures involved, all of which constitute a large number of *coordinated* adaptations. It is obvious, therefore, that the phenomena of responsiveness and adaptation are very closely associated since it is only through mechanisms of the former that the latter is made possible for an organism.

10.3 The study of organisms in relation to their environments is within the province of *ecology*. Since the various adaptations exhibited by organisms are important to them in terms of their surroundings, it is essential that the student of biology understand something of ecological principles which have been formulated and which lend meaning to the overall phenomenon of adaptation.

**Organisms
and**

environment

The environment of an organism not only includes its physical surroundings, but also such other organisms as may be present, which means that any influences they exert upon each other must be taken into consideration. For purposes of discussion, therefore, we shall distinguish between environmental factors that are *physical* in nature, those that are *biogeochemical*, and those that are *biotic*.

The physical environment One of the most important environmental factors to which organisms are subjected is *light*. This should be obvious in the case of green plants since they are dependent upon sunlight as an energy source in the photosynthetic process. The leaves of higher plants are adapted in various ways to sunlight; in many cases, they are arranged on the plant in such a way that maximum exposure to sunlight is realized. However, the influence of light is not limited to photosynthetic effects; the flowering process in many plants is rigidly controlled by the time pattern and quality (wavelength) of light received. One example of such control is *photoperiodicity*, or the response of an organism to the length of time it is exposed to light. The principle of photoperiodicity is exploited by

commercial nurserymen in producing blooms out of season. By supplying artificial light or by subjecting plants to periods of darkness, as the case may be, it is possible to regulate the time of flowering. For example, chrysanthemums may be grown under photoperiodic conditions that result in their blooming at seasons when demand for them is great. Some species are termed *long-day* plants, because they normally bloom only when days are long, whereas others are called *short-day* plants, since they respond in their flowering processes to shorter periods of light. As might be expected, there are species which are intermediate in their light requirements for the development of flowers, and there are some whose flowering process is not influenced at all by length of light exposure. In addition to the regulation of flowering, a great many other light-controlled processes are known in plants, some of which are seed germination, leaf fall, the development of color in leaves, and growth rates of plant organs.

A number of adaptations to light are also seen in the animal kingdom, among the most obvious of which are the eyes of higher animals. Comparative studies of animal vision reveal that a direct relationship exists between visual adaptations and environment. For example, bees and most other insects are apparently "red blind," whereas red is a particularly vivid color to birds. This, in turn, is reflected by the adaptations of flowers and berries. Most insect-pollinated flowers are not red, whereas many which depend upon birds for pollination are. Furthermore, the berries and fruits of many plants are red, as a consequence of which birds are attracted to them. Such species may become widely distributed, since birds ingest and later eliminate many seeds. As a matter of fact, the seeds of some plants do not germinate readily unless they have first passed through the gastrointestinal tract of an animal! This illustrates how far-reaching one factor of adaptation may be (remember, we started out talking about light). Again, the eyes of nocturnal animals such as cats and alligators have extremely sensitive light receptors. These receptors are protected from daylight intensities by slit pupils, which admit far less light than round pupils. In addition, important aspects of animal behavior such as mass movements, reproductive activity and feeding habits are influenced tremendously by light.

Another important factor of the physical environment is *temperature*. If a survey is made of plants and animals that exist at various temperature zones of the earth, it is found that there is a direct correlation between this factor and those features which adapt organisms to their respective habitats. For example, tropical palms and grasses lack the protective tissues which would ensure their survival in freezing temperatures, and alpine plants (those growing



(a)



(b)

Figure 10.3 A striking adaptation to seasonal changes is seen in the willow ptarmigan (a) winter plumage; (b) summer plumage. (Charles J. Ott, from National Audubon Society.)

above the timberline on mountains) adapted to cold climates do not grow in the tropics. Many animals are adapted to seasonal changes, and in some cases even change their camouflage patterns (Figure 10.3). In addition to its influence upon animal and plant distribution, temperature is of considerable ecological significance in other ways. Seeds of most plants do not germinate until the temperature is fairly warm; some will not germinate even at the proper temperature unless they have previously been exposed to a period of cold. One rather unusual adaptation to temperature is seen in the case of seed cones of the jack-pine (*Pinus banksiana*), which do not open readily to release the seeds until they have been scorched by fire. Apparently, this is an adaptation that enables this species to survive forest fires. Among animals, temperature is an important factor in reproduction, rate of embryonic development, migratory activities, and a great many behavioral characteristics. As an example of temperature adaptations in animals, the birds and mammals are able to maintain constant body temperatures by virtue of a feature of the nervous system which is absent in "cold-blooded" animals. This is the *temperature-regulating center* of the brain, a kind of built-in "thermostat." This feature, plus accompanying heat-regulating adaptations such as the feathers and hair exhibited by these two groups of animals, respectively, makes it possible for them to exist under a wide range of temperature conditions.

Water is another factor that is ecologically important. Some organ-

isms possess adaptations that make it possible for them to live entirely within an aqueous environment, whereas others are adapted to land. Structural adaptations in these respective environments are frequently quite obvious; gills of fishes and lungs of land vertebrates are among those that are better known. We have mentioned the contractile vacuoles featured by many unicellular freshwater organisms which are adaptations to osmotic pressure. In oceans, it has been observed that certain species are characteristic of various depth zones, indicating adaptations for withstanding pressures that exist at different levels of the sea. Organisms that live on land are adapted variously to water; some plants and animals are restricted to moist environments, while others inhabit only dry areas. Cacti are typical plants that possess features making possible their existence in desert areas, and among animals, the camel and the kangaroo rat (Figure 10.4) have become almost proverbial for their capacity to withstand dry conditions.

In addition to these physical factors, a number of others assume great importance. Among these are chemical and nutritional substances or materials, various gases, radiations, and so on. In general, however, light, temperature, and water may be considered the most important physical factors of the environment.

It should be pointed out that these environmental factors are merely separate parts of a total situation, and they frequently exert



Figure 10.4 A kangaroo rat in its natural desert habitat. This animal does not have to drink at all; its metabolic water is sufficient to satisfy its minimal requirements. (Woodrow Goodpaster, from National Audubon Society.)

effects together. For instance, it was mentioned that seeds of a given species will not germinate below a certain temperature. However, even if an ideal temperature is provided, there will be no germination unless enough moisture is present to activate enzymes and to enter into reactions within cells of the embryonic plant. In this case, neither temperature nor water are independent of each other; a seed is adapted to germinate only when certain conditions of both factors are met. Similarly, the temperature of an environment may be ideal for some animal to exist successfully, but if its water needs are not met, it cannot survive. This important principle is called the *law of the minimum*, and stated more precisely, it holds that regardless of how satisfactory one or more requirements of an organism may be, it cannot survive unless all requirements are met. As a further example of this "law" and its application, let us suppose that a certain plant is supplied with all physical and chemical requirements in adequate amounts except one essential element (for example, manganese). Regardless of how adequate other environmental conditions may be, the *minimum* requirements of the plant have not been met, and it cannot survive. Put in terms of an analogy, a chain is no stronger than its weakest link. If the list of requirements for a given organism (both physical and chemical) be considered a chain, and if only one item is missing, then the rest of the chain is worthless in terms of keeping the organism alive.

Biogeochemical factors of the environment Since plant and animal bodies are composed of matter, they depend upon their surroundings for those elements which make them up and keep them alive. Significantly, matter is not ordinarily lost to the world of life with usage; a given atom of carbon, for example, may have been a part of numerous different plant and animal bodies throughout time. Since the atoms of such elements may be used over and over, we say that they travel through *cycles*. Because certain phases of a given elemental cycle may involve other factors than purely biological ones, we refer to the entire pathway as a *biogeochemical cycle*, a term which tells us that biological, geological and chemical factors are all involved. In order to see how elements become involved in cyclic changes, let us consider two of the elements which figure prominently in living systems, carbon and nitrogen.

A carbon cycle is shown in Figure 10.5, where it will be seen that atmospheric carbon dioxide serves as the carbon source for the synthesis of organic compounds in autotrophic plants. Animals, in turn, are ultimately dependent upon plants for their organic compounds. Further anabolic and even catabolic changes may occur which keep carbon "trapped" within organic compounds, and some may be lost to the cycle for long periods of time. Coal and oil de-

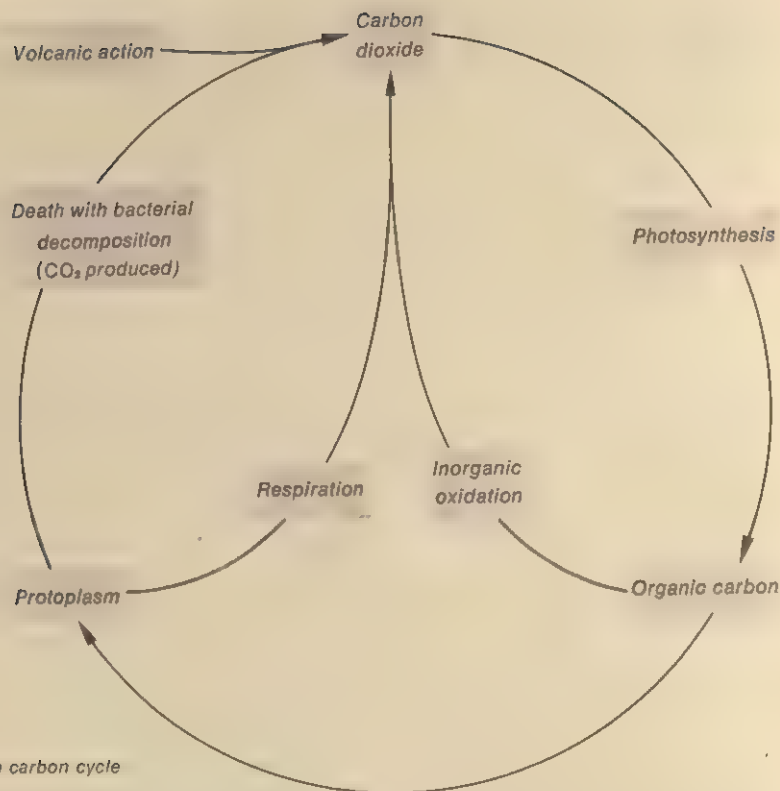


Figure 10.5 A schematic representation of the carbon cycle in nature.

posits, for instance, were formed many millions of years ago from plant and animal bodies, and the carbon involved is of necessity not available until these materials are either burned or decomposed. Eventually, however, the trapped carbon may be returned to the atmosphere by this means in the form of carbon dioxide. Ordinarily, of course, carbon gets back into circulation within a relatively short period of time through respiration of plants and animals and through processes of decomposition. Although of limited importance in a quantitative sense, volcanic eruptions contribute carbon dioxide to the atmosphere. Through the interaction of these various processes, which we have illustrated as a cycle, carbon is used over time and time again by living forms.

Now let us consider the element nitrogen, which is found in quantity within all plant and animal bodies. It is not present as molecular nitrogen (N_2), of course, which is a gas; rather, it is an essential part of proteins and certain other types of organic molecules. A nitrogen cycle is shown in Figure 10.6, where it will be seen that plants and animals, along with their waste products, eventually undergo

decomposition. Of course, just as carbon may be trapped in organic molecules for long periods of time, nitrogen may become temporarily unavailable at some point of the cycle. At any rate, the nitrogen of waste products and dead bodies eventually appears in the form of ammonia (NH_3). Further bacterial action makes possible the formation of nitrites (NO_2 compounds) and then nitrates (NO_3 compounds). In the latter form, nitrogen becomes available to green plants, which combine it with photosynthetic products in the synthesis of plant proteins. It should be noted that a lesser cycle occurs between nitrates and atmospheric nitrogen; nitrates may be decomposed by certain bacteria in soil and water to release gaseous nitrogen to the atmosphere, which is something of a "loss" to the main cycle. However, this loss is partially compensated for by the phenomenon that lightning converts gaseous nitrogen to nitric acid (HNO_3) which becomes deposited in the soil, and by the ability of certain bacteria and algae to "fix" gaseous nitrogen in the form of organic compounds. As Figure 10.6 shows, nitrate nitrogen may become incorporated into plant proteins and thus complete the cycle as we have described it.

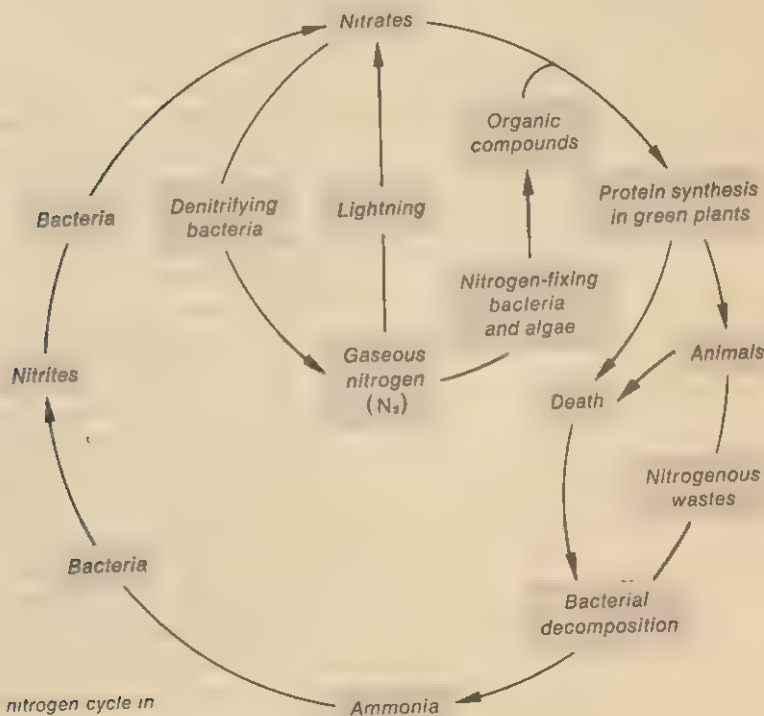


Figure 10.6 A schematic representation of the nitrogen cycle in nature.

Carbon and nitrogen are only two of the many elements that undergo cycles of this sort, and their changes in form may be considered typical of others. Because these cycles function as they do, there is made possible a constant reuse of matter. In this sense, therefore, matter is conserved; energy may be lost, organisms die, and species undergo changes, but the fundamental units of matter travel their cycles in unending fashion.

Biotic factors of the environment A given organism may be influenced by two other groups of organisms: those that are members of its own species and those that are not. There is at least one essential relationship which must exist among members of most sexually reproducing animals, for example, that of copulation. A great many adaptations are seen in both the animal and plant kingdoms which allow for biparental reproduction. Some of these are highly specialized. For example, as we have mentioned, certain animal species are characterized by highly complex courting rituals that are concerned with mate selection and subsequent production of offspring. With regard to essential requirements such as food (in the case of animals) and sunlight (which is necessary for food synthesis in green plants), members of the same species are frequently found to be in *competition* with one another. One of the most fundamental of all ecological principles is that the reproductive potential of a species tends to run far ahead of its food supply or available space, and it is inevitable that some members survive at the expense of others. As we shall see, this principle plays a very important part in the establishment of new adaptations in species. Some species are so organized that *cooperation*, rather than individual competition, is exhibited. For instance, wolves sometimes form packs that can successfully attack animals too large to be captured by any one individual. This type of cooperative group is called an *aggregation*. A much more highly organized cooperative unit is the *society* (Figure 10.7), which achieves its highest degree of specialization in certain insect species.

In the consideration of relationships that exist between members of different species, competition is of great ecological importance. Plants of different species compete in nature for sunlight and root space; animals whose food or shelter requirements are similar may be in keen competition, especially when food or space become scarce. Perhaps the most important ecological consideration of inter-specific relationships, however, is the principle of the *food chain*. Essentially, a food chain is a series that begins with a chemical medium, either soil or water, within or upon which photosynthetic *producers* serve as food for varying numbers of animal *consumers*. For example, in a typical freshwater pond, the producers are various algae and perhaps some aquatic seed plants. These support

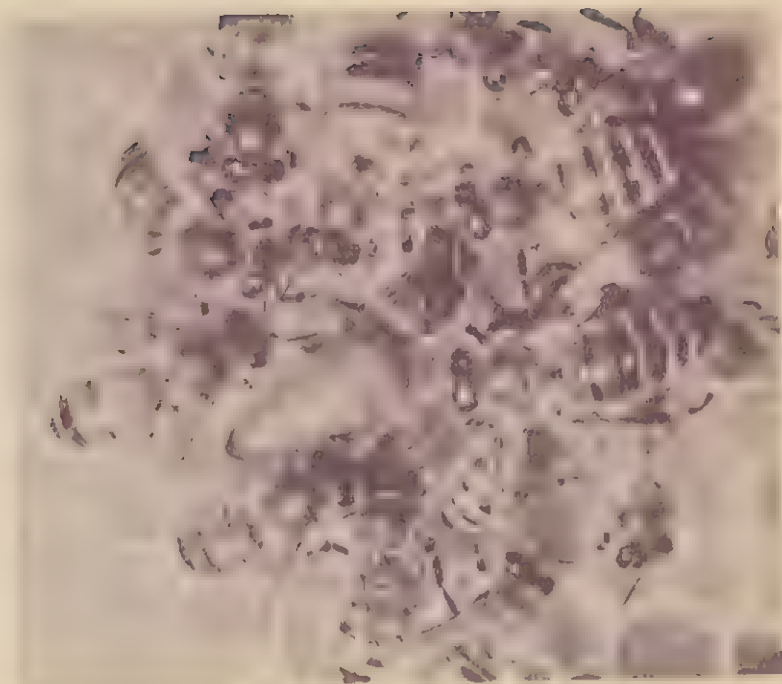


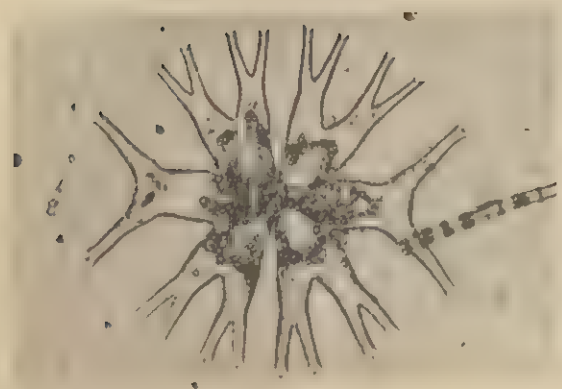
Figure 10.7 Queen bee and her "court."
These and other social insects show a
high degree of intraspecific coordination.
(© Walt Disney Productions.)

certain microscopic animals which, along with the algae, constitute a mass of small, living forms collectively known as *plankton* (Figure 10.8). Certain fishes, especially small forms, are adapted to live upon plankton by virtue of mechanisms which strain these organisms out of the water as it passes into the mouth and over the gills. Eventually these fishes are eaten by larger forms which may in turn be eaten by others, and so on. Hence, there is a chain beginning with the nutritive medium and ending with the ultimate consumers. Eventually, of course, the consumers themselves die (assuming that they are not removed from the pond), and they may figure prominently in the same food chain or in a different one. Somewhere along the line, animal materials are decomposed by bacteria or fungi, and the products of decomposition (for example, carbon dioxide and ammonia) are made available to the producers. In fact, materials of dying and dead organisms and their wastes are decomposed by bacteria and fungi throughout the chain.

Food chains necessarily involve *predation*, or the feeding of certain forms on others. Except for a few species of plants such as the Venus fly-trap, which we have mentioned, predators are all animals. Two classes of predatory animals are generally recognized, *carnivores* are adapted to feeding on other animals and *herbivores* to



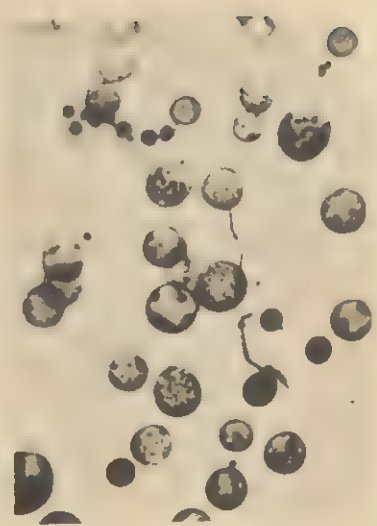
(a)



(b)



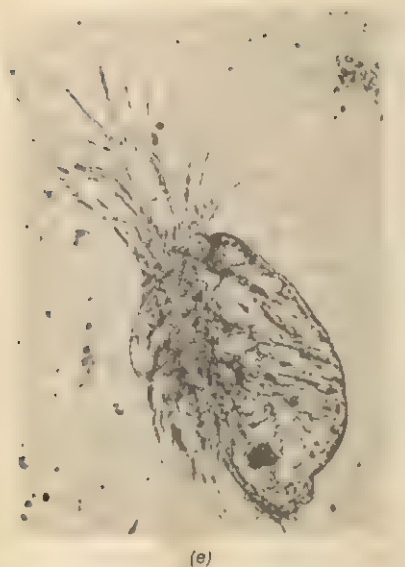
(c)



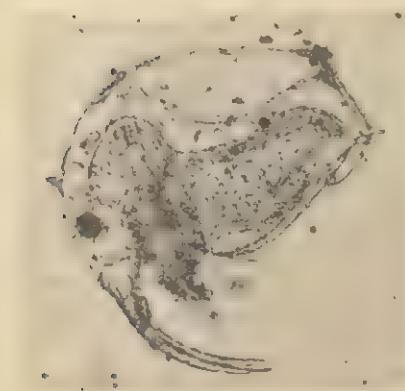
(d)

feeding on plants. Some species exist on a mixed diet, however, and thus a third group, the *omnivores*, may be recognized. Predation is frequently thought of as a somewhat unpleasant side of nature, and many persons build up some rather anthropomorphic views with regard to carnivorous animals. Hence, a lion is often pictured as a "bad" animal, and a sheep is evaluated as a "good" one. Some people actually think that a carnivore is capable of making value judgments, and "ought" not to kill and devour other animals since this is cruel and wicked. What these people fail to see is that an animal which is adapted through heredity for a carnivorous existence cannot be expected to shake off these structural and functional limitations and start eating grass. Their behavior, at least with respect to the acquisition of food, is quite determined. Furthermore, predation is not as bizarre a phenomenon as some people might think. In the first place, many plants and small animal forms, which apparently lack any sort of consciousness, are involved. They are no worse off for having been eaten than a rock is for having been broken. As for higher animals, there is no reason to believe that they are capable of the mental anguish with which human beings regard death. Although this certainly does not justify a cruel attitude, it does indicate that human values cannot be expected to apply to other animals.

Aside from such considerations as these, predation is very important in the maintenance of natural populations. We mentioned that reproductive potential in organisms runs far ahead of available food and space; were it not for predators, animals and plants would overproduce, and certain forms would become extremely numerous. Such an imbalance is often seen when normal population ratios of nature are upset in some way. For example, the coyote of the western United States is generally regarded as a very harmful predator because it sometimes eats livestock. When it is excessively hunted by man so that numbers of individuals are greatly reduced in a given area, the result is usually one that is ecologically worse for man than the former situation. With the decline of the coyote population, smaller animals upon which they would normally prey increase in number until they become more detrimental than coyotes. The natural prey of coyotes is the rabbit, whose reproductive potential is proverbial. Within a short time after the disappearance of coyotes in a given area, rabbits generally increase to such an extent that they



(e)



(f)

Figure 10.8 A variety of typical plankton organisms (a, b) Two desmids (unicellular green algae) (c) A diatom, which is still another type of unicellular green alga. (d) Several colonial green algae (e, f) Two types of microcrustacean (arthropods). These photographs represent various magnifications.

consume pasture grass and other plants that support livestock. The rancher may thus be choosing the worse of two evils when he destroys coyotes. To cite another example, hunters sometimes urge the eradication of wolves and mountain lions because they prey upon deer. Studies have shown quite clearly that, in the long run, predators exert a favorable influence upon the long-range survival of deer populations. For the most part, they prey upon the old and diseased animals, thus eliminating the most dispensable members of the herd. Almost without exception, the elimination of predators has led to difficulties in maintaining healthy herds of deer.

Organisms of different species often become closely associated in their environmental adaptations, and these relationships are of special interest to the ecologist. One such relationship is that of *mutualism*, wherein two associated organisms belonging to different species both derive benefit from living together. We have observed that a lichen is composed of an alga and a fungus, both of which are adapted to live under conditions where neither could exist separately. The alga is able to furnish photosynthetic materials to the fungus, while the fungus provides a suitable environment for the alga by supporting its cells and by holding water which it can use. We also mentioned the association of cellulose-digesting protozoa with termites, an arrangement that enables these insects to subsist on wood. At the same time, the protozoa are provided with a place to live, and they also receive essential materials such as water and inorganic salts from their mutualistic partners. Another type of relationship is that of *commensalism*, in which two members of different species are so associated that one derives benefit while the other is neither harmed nor helped. It is common, for example, to find barnacles (which are arthropods) attached to the shells of mollusks or to other arthropods, and some even attach to the skin of whales. By virtue of this arrangement, a given barnacle may take in bits of food that drift away from the other organism when it eats, and in terms of species distribution, it may be carried to points it could not possibly reach otherwise. At the same time, it does no harm to its partner organism. A third important special relationship between members of different species is that of *parasitism* in which one member (the parasite) derives benefit at the expense of the other (the host). Man, for example, is host to a number of parasites such as tapeworms and various bacteria. In their nutritive requirements or in the production of metabolic wastes, they may cause serious damage to organs or tissues of the host. Parasites such as these, that live within the body of the host, are known as *endoparasites*. Others, called *ectoparasites*, exist upon the bodies of animals or plants. Lice, ticks, and leeches are representative ectoparasites.

10.4 Ecosystems, food chains, and energy From one point of view, biology might be termed the study of differential levels of organization. We have seen how new characteristics emerge with each new level; from atoms to organisms, the qualities of successively higher levels demonstrate rather clearly that in living systems a whole is more than the mere sum of its parts.

To the ecologist, the primary biological unit of interest (that is, the basic level of organization) is the *ecosystem*. This term is used to describe all the component parts of any certain area, both living and nonliving. For example, a given lake is an ecosystem. As a unit, it consists of all the living organisms associated with the lake in any way, the dead and decaying organisms, the water, dissolved gases and minerals, the atmosphere above the water, and even physical factors like light and temperature. Although a given ecosystem is a distinct unit, there may be considerable overlap from one ecosystem to another. For instance, two lakes some miles apart would be studied as two distinct ecosystems, and yet the same birds might frequent both lakes. Certainly, the same sun furnishes energy to both. An ecosystem, then, is not so much an absolute segment of nature as it is a unit of convenience for ecological study.

Depending upon the viewpoint, an ecosystem may be studied in a variety of ways. For our own purposes, however, we shall restrict ourselves to a consideration of food and energy relationships as they are demonstrated in ecosystems.

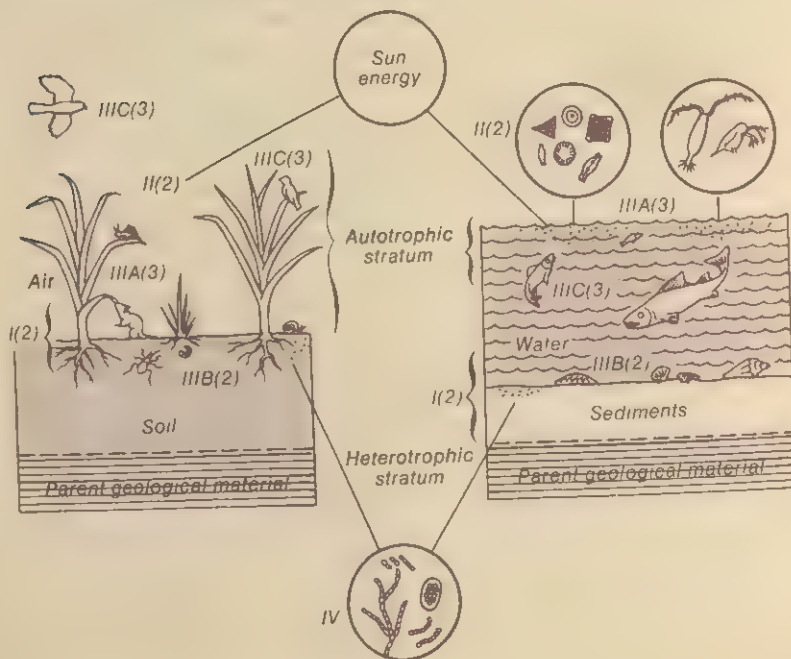
We have seen that conversions of matter from one form to another are essentially cyclic, as illustrated by the carbon and nitrogen cycles (Figures 10.5, 10.6). In contrast, energy conversions travel a one-way street (although they may be detoured temporarily). To illustrate, the catabolism of a mole (gram-molecular weight) of glucose by the human body results in the generation of some 38 moles of ATP from ADP and phosphoric acid. This does not represent all the chemical energy of the glucose; the remainder is lost as heat. Eventually, the ATP is "spent" on movement, active transport, synthesis, and so on, and at each step more heat is lost. Presumably, with successive transformations, all the energy is eventually lost as heat. Consequently, if the body is to have access to more energy, it must catabolize more glucose (or some other food substance). This is entirely consistent with the laws of thermodynamics and is, in fact, an excellent demonstration of their validity. You will recall that the first law holds that energy is neither created nor destroyed, although it may be changed from one form to another. It does *not* hold that energy cannot be lost from a system, even from the entire planet upon which we live. The second law holds that energetic systems

tend toward increased entropy (randomness), such as occurs when the relatively ordered and concentrated potential energy of ATP becomes the relatively disordered and dispersed kinetic energy of heat. This is why no energy transformation can be 100 percent efficient. Perpetual motion is as impossible in living systems as it is in mechanical systems.

When we view ecosystems in the light of thermodynamics, a number of relationships among organisms and between organisms and the environment become quite clear. This is an essential starting point in ecology; once basic energy relationships have been grasped, one can meaningfully study segments of ecosystems, such as populations, from any number of ecological standpoints.

A comparison of two contrasting ecosystems Let us consider the basic features of ecosystems by comparing a terrestrial ecosystem with an aquatic one (Figure 10.9). In each case, as is generally true of ecosystems, four types of component exist: (1) *nonliving*, or abiotic, materials such as water, dissolved minerals, and soil components; (2) *producers*, which are autotrophic plants; (3) *consumers*, which are chiefly animals; and (4) *decomposers*, which are chiefly bacteria and various fungi. Although the specific nature of each category of components differs in our selected contrasting ecosystems, their functions are essentially the same in each case. The abiotic materials

Figure 10.9 Comparison of the gross structure of a terrestrial ecosystem (a grassland) and an open-water ecosystem (either freshwater or marine). Necessary units for function are the following: (I) abiotic substances (basic inorganic and organic compounds); (II) producers (vegetation on land, phytoplankton in water); (III) macroconsumers or animals: (A) direct or grazing herbivores (grasshoppers, meadow mice, etc., on land, zooplankton, etc., in water), (B) indirect or detritus-feeding consumers or saprovores (soil invertebrates on land, bottom invertebrates in water), (C) the "top" carnivores (hawks and large fish); (IV) decomposers, bacteria and fungi of decay. [Adapted by permission from E. P. Odum, *Ecology* (New York: Holt, Rinehart & Winston, Inc., 1963).]



found in each type of environment are roughly the same, although a considerable difference in relative proportions exists. Obviously, the producers in a pond differ greatly from those on land. In water, they are algae and a few rooted plants, whereas on land they are almost exclusively rooted plants. An even greater contrast is seen in the consumers. In the water, the *primary* consumers are mostly insect larvae, small crustaceans, and small fish, and the *secondary* consumers are mostly fish which feed on the primary consumers. On land, there is a wider variety of primary consumers, ranging from such small invertebrates as snails and insect larvae to such large herbivores as sheep and deer. A variety of secondary consumers, the carnivores, feed on the herbivores. Finally, the decomposers in each case are bacteria and fungi, but each type of ecosystem has its characteristic species.

In each type of ecosystem, as in all ecosystems, sunlight is the primary energy source. Although any given producer is efficient in converting radiant energy to chemical energy, the amount of light available to an ecosystem is enormous as compared to that actually utilized. It has been estimated that much less than one per cent of the total energy reaching a given ecosystem is actually "fixed" as chemical energy. Of this amount, a certain portion is expended in the metabolism of the producer, so that even less is available to the primary consumer. We shall take a closer look at the transfer of energy from organism to organism in the next section, but our point of emphasis here is that the source of energy is the sun and that **synthesis (production) is obviously endergonic.**

Food chains and trophic levels In an earlier section, we introduced the concept of a food chain to illustrate relationships that exist in nature between members of different species. Let us now examine this concept from a different standpoint, that of energy transfer within the ecosystem.

In consideration of food chains, it is convenient to speak in terms of *trophic levels*. The word "trophic," you will recall, is roughly a synonym for "nutritional" (Gr. *trophikos*, nursing). To illustrate its usefulness, let us return momentarily to our two contrasting ecosystems, discussed above. In each case, the producers are at the same trophic level. However, consumers may occupy different trophic levels. For example, in the pond, a primary consumer such as a crustacean might feed on algae, then serve as food for a fish which is thus a secondary consumer. This secondary consumer might then serve as food for a larger fish, or tertiary consumer, and finally, the ultimate consumer (perhaps a bird) would feed upon the tertiary consumer. Now let us assume that in the terrestrial ecosystem there is only one consumer, perhaps a horse. Obviously, the horse and the

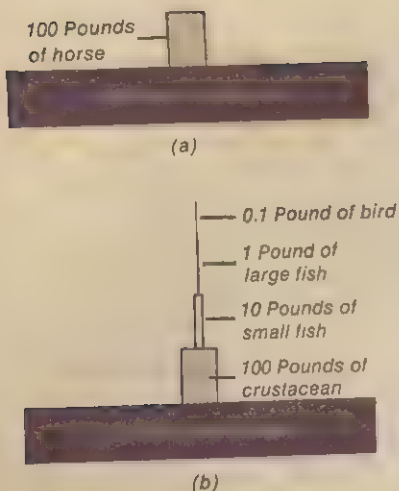


Figure 10.10 A graphic representation of the principle of the food chain or pyramid of numbers. At (a) a 10-percent yield from the producer results in 100 pounds of consumer weight. The same is true at (b) of the primary consumer, but the ultimate consumer in this chain realizes only a 0.1-pound, or a 0.01-percent, yield from the producer.

bird in these two situations occupy different trophic levels, and each stands at the top of a food chain of different length to the other.

Since there is considerable energy loss between trophic levels, a general nutritional principle may be stated: *The longer the chain, the less there is to show for the energy captured by the producers.* Although rates of loss from one trophic level to the next vary from one food chain to another and in different ecosystems, it is a fairly safe rule-of-thumb to assume a 10-percent rate of retention as expressed by weight. At least, we can use this figure for illustrative purposes. If there is such a reduction in the two chains introduced above, then, we can see immediately how the principle stated above applies in each situation. For instance, 1,000 pounds of grass will produce 100 pounds of horse, and 1,000 pounds of algae will produce 100 pounds of crustaceans. In the longer chain, the total mass of the birds will obviously be less than that of the horses in terms of equivalent weights of producer organisms. Because food chains result in smaller amounts of energy available at each level, which is reflected in total mass, a food chain shown in quantitative terms is called a *pyramid of numbers*. Figure 10.10 demonstrates the two contrasting pyramids we have discussed.

It would be very difficult to overemphasize the biological significance of this ecological principle. For one thing, it demonstrates the operation of thermodynamic laws at the highest level of biological organization, thus substantiating the concept that the physics and chemistry of living systems are not fundamentally different from those observed in the nonliving world. Again, it is possible to understand in the light of this principle why extremely large animals are usually found at the end of a very short food chain. The largest land animals, such as the elephant and the rhinoceros, are entirely herbivorous, and the largest whales feed exclusively upon plankton. Apparently, such an animal as a 100-ton blue whale can maintain its bulk only if great quantities of food are available for a minimum of effort. Only producers or possibly primary consumers ordinarily meet these qualifications.

Although the food chain—pyramid of numbers principle is of limited practical concern to man as long as it merely goes on in nature, it is extremely important in its bearing on human nutrition. After all, man is the ultimate consumer in a number of possible food chains, and the pyramid of numbers is important in an economic sense. For example, everything else being equal, it is far cheaper to exist upon vegetables than upon meat because there are no intermediate consumers when man himself feeds upon products of photosynthesis. Another important consideration is that, as the human population expands, the food problem increases. Hence,

there is great interest in the development of methods whereby man can utilize more producers (such as algae) directly, and it may be largely through studies of fundamental ecology that future problems of human nutrition will be solved, if they are.

As they actually operate in nature, food chains are not isolated systems. Rather, they form interconnected patterns called *food webs* (Figure 10.11), and we introduced this concept earlier (Section 4.2)

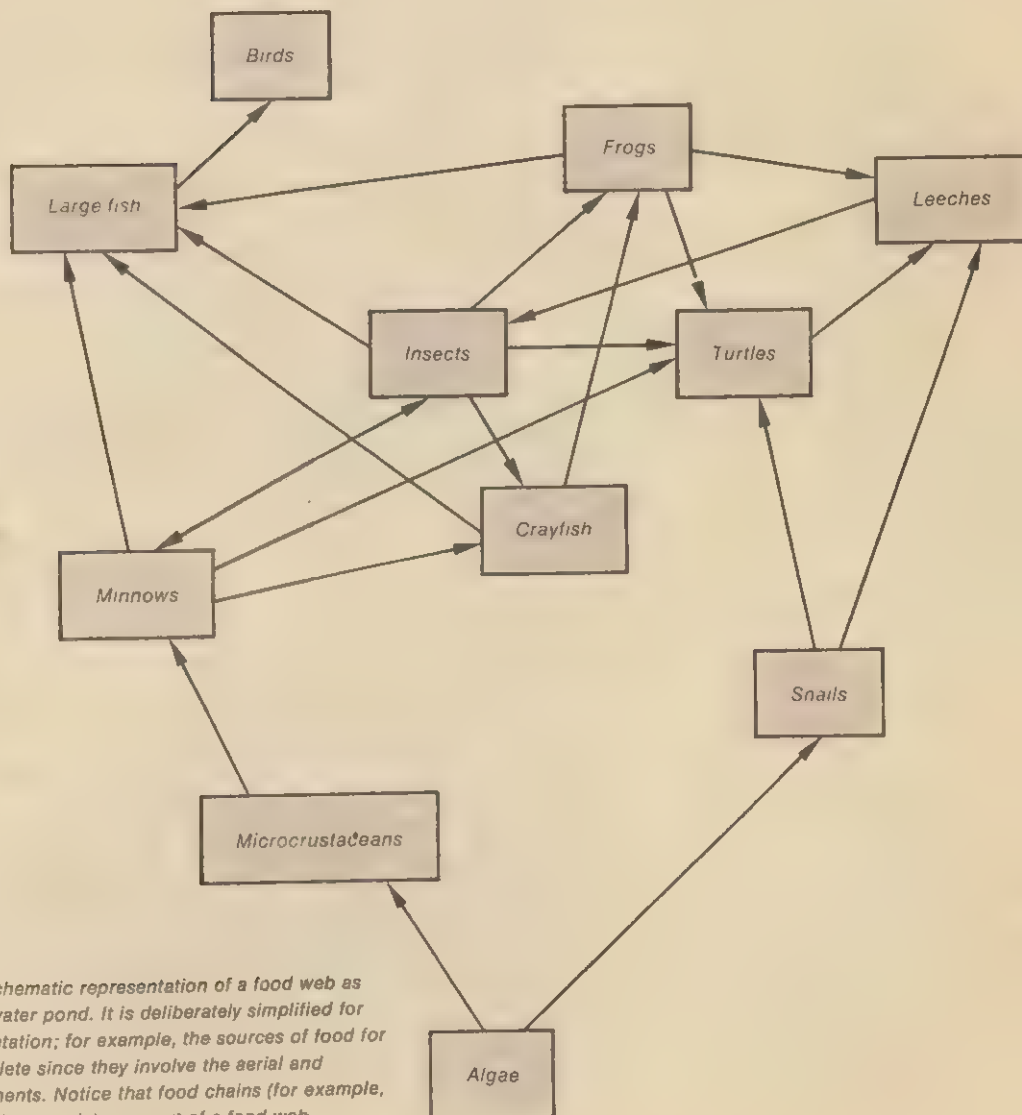


Figure 10.11 A schematic representation of a food web as it exists in a freshwater pond. It is deliberately simplified for purposes of presentation; for example, the sources of food for insects are incomplete since they involve the aerial and terrestrial environments. Notice that food chains (for example, from algae to birds) may exist as a part of a food web.

when we discussed the diversity of organisms. Nevertheless, a food chain constitutes a convenient device for studying biological productivity, just as the ecosystem is a convenient unit for studying ecological relationships. In both cases, they are somewhat artificial representations of what actually occurs in nature.

10.5 Summary

Adaptation is the characteristic of living forms to develop, over time, certain structural and functional features which enable them to survive and reproduce within the limits of a particular environment. As a process (discussed in the next chapter) it has given rise to many structural and functional *adaptations* to environmental circumstances.

Ecologists recognize three classes of environmental factors: those which are physical, such as light, temperature, and water, those which are biogeochemical, such as the elements involved in protoplasmic synthesis, and those which are biotic, that is, other organisms. A number of types of relationships among organisms reflect the complexity of especially biotic factors.

In terms of their nutritional requirements, organisms may be related to each other according to trophic levels. The organisms occupying any given trophic level in an ecosystem capture only a fraction of the energy represented by the next lower level. So a short food chain is more productive than a long one in terms of energy conservation. In nature, food chains are interconnected parts of a more complex nutritional pattern, the food web.

Questions

1 In what sense is adaptation a *process*? In what sense may adaptation be the *result* of a process?

2 Over the years, many states have paid bounties for the killing of predators. In the light of this chapter, what do you think of this as a general practice? Can you think of any circumstances where such a practice might be justified?

3 Define the following and give an example of each: aggregation, society, mutualism, commensalism, parasitism.

4 Certain bacteria of the soil are called *denitrifying bacteria* (see Figure 10.6) and still others are called *nitrate reducers*, that is, they convert nitrates to nitrites. Why would each type be considered detrimental to man's interests from an agricultural viewpoint?

5 If ecosystems and food chains are so indistinct as to be termed "somewhat artificial," how can they be of sufficient value to ecology that they merit consideration?

6 If red flowers or berries are important to the survival of certain

plants, as we implied in discussing the color vision of birds, what explanation might be given for the fact that many successful plant species are not characterized by any red parts at all?

7 What is the "law" of the minimum, and why do you suppose the word "minimum" is used in its wording?

8 Production of large fish in a freshwater pond may be increased by the addition of fertilizers. Commercial fertilizers are usually a mixture of salts of nitrogen, phosphorus, and potassium plus certain inert materials and trace elements. How can you account for the increased production of fish?

9 The ecologist M. Kleiber has estimated that if a man lived on chicken eggs alone for a year, about 7 acres of land would be required to feed him. In contrast, enough grain could be raised on 0.3 acre to feed a man for a year, and only 0.002 acre would be required if he subsisted only on algae. Explain these figures in terms of the food chain-pyramid of numbers concept. Can you suggest an explanation for the considerable difference in the areas required for raising grain and algae?

10 In commenting upon industrial wastes, radioactive fallout, and various other man-made factors as they affect the environments of the world, the contemporary biologist René Dubos states:

Despite all the new powers of science, or perhaps because of them, man is no longer able to achieve real mastery over his environment. . . . We are approaching the stage, if we have not already reached it, where science will be unable to fulfill one of its major duties, namely to predict and control the consequences of human intervention into the processes of nature.

[*The Great Ideas Today* (Chicago: Encyclopædia Britannica, Inc., 1964).] Does this indicate a need for more emphasis upon ecological principles and their application in our society? Discuss the implications of this statement.

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Phillipson, J. Ecological Energetics. New York: St. Martin's Press, Inc., 1966. This very brief presentation emphasizes the energy changes which occur in nature, with special emphasis upon ecosystems and productivity.

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The concept of evolution

So far in this book, we have devoted attention almost entirely to phenomena which are demonstrable at the present time in nature. In a few instances, we have introduced the concept of evolution to explain some existing phenomenon, but we have deliberately chosen to defer a detailed discussion of this subject until we were able to establish some basis for understanding it. Evolution is a difficult concept to grasp, even for professional biologists. And yet, it is imperative that we view biology through this concept; otherwise, it is impossible to coordinate the major principles of biology or to interpret them meaningfully. This is particularly true of adaptation, which we introduced in the preceding chapter. For example, we may recognize the existence of water-conserving mechanisms in desert plants, and we may interpret their ecological significance correctly. Sooner or later, however, if adaptations or adaptation (the process) are to be understood, the question of origins must be asked and answered.

Because the process of adaptation is basic to evolution, we shall discuss some of its mechanisms later in the chapter. However let us first make certain of our definitions and introduce some relevant data.

- 11.1** Fundamentally, there are two possible explanations for the origin of adaptations: *special creation* and *organic evolution*. According to the concept of special creation, a supernatural force or personality fashioned and designed the great variety of plants and animals, along with the adaptations peculiar to each species. Hence, there is postulated the existence of a Creator who served at some time as a cosmic engineer, carefully working out structural and functional needs of organisms as they would need them in their chosen environments. As late as the middle of the nineteenth century, most biologists were special creationists. In the main, they were content to explore the descriptive side of biology and to accept the authority of established religions as to origins. This accounts for the fact that taxonomic systems were rather artificial since the idea of actual genetic kinship was largely foreign to the thinking of the times. Actually, creationism is a convenient way of ignoring the whole problem since it avoids biological explanations rather than providing any

The concept of organic evolution is one of biological *change*. Essentially, it holds that present-day organisms are the descendants of ancestors that were, at some stage of time, more simple in organization. Biologists use the term evolution in at least three different senses. As we have employed it above, it is a *concept*, or viewpoint, by means of which nature may be interpreted or explained, just as special creation is a concept. In terms of scientific endeavor or procedure, evolution is a *theory*, whose validity depends upon its success in predictability. (Why is special creation not a theory?) In

terms of a series of historical events subject to analysis according to accepted historical methods, evolution is a *process*. Since we shall be using the term in all of these contexts, it is extremely important that we keep these distinctions in mind.

Although the concept of evolution as defined above simply means that nature is not static, but is subject to continuous change, certain implications necessarily follow. Since life had to start *some-where*, it is generally regarded by evolutionists that either once or many times, organization of chemicals occurred in some way so as to result in a quantity of matter that was alive. From this point on, species developed through change and the inheritance of change until the present time. Let us notice that the concept of evolution does not rule out the idea of God, nor is it *completely* irreconcilable with the concept of special creation. One might believe very strongly (and some biologists do) that the primary organization of protoplasm or at least the formulation of physical law governing the process was a supernatural event. It might even be held that a small number of species were divinely created, and that these gave rise to others, an idea which would still represent acceptance of an evolutionary concept in explanation of the origin of species and their various adaptations.

However, most evolutionists believe that life originated in some fashion within the primeval seas, and that present-day forms are the results of these humble beginnings. This is not entirely a matter of speculation. For reasons that depend upon evidences from physics and geology, it is believed that great quantities of water, methane, hydrogen, and ammonia existed on earth more than 2 billion years ago. Atmospheric conditions were such, apparently, that electrical discharges in the form of lightning occurred with great frequency. Within recent years, experiments have been devised that attempt to reproduce these environmental circumstances under laboratory conditions. If water, methane, hydrogen, and ammonia are placed in a closed container and subjected to electrical discharges for several days, analysis of the original mixture reveals the presence of several organic compounds that are normally associated only with life! This experiment has been repeated successfully many times, and it indicates strongly that compounds essential to the organization of protoplasm could have developed by natural means. Chance reactions between such compounds, occurring over tremendous periods of time, may well have produced nucleoprotein molecules capable of self-duplication. In the midst of a nutritious sea of organic compounds, living systems quite possibly had their beginnings when these nucleoproteins "learned" to accumulate proteins around them. The first living organisms, therefore, may have been somewhat

similar to modern viruses (Figure 3.1). Through mutation (Section 11.3) and other processes of evolution, they eventually gave rise to more complex descendants.

In consideration of this concept, two important factors should be kept clearly in mind. The first is that time, measured in terms of hundreds of millions of years, was available. Now this does not mean that time alone can account for any phenomenon, unless combinations or reactions are possible, it matters little whether a century or a billion years are available. However, it has been shown how organic molecules were possibly formed under the existing conditions, and we know that organic molecules can react with one another and with inorganic substances. Perhaps it was simply a matter of time until the "right" combinations occurred, which enabled a relatively simple organism to make more of itself from the surrounding medium. The second factor of importance to our discussion is that the primeval environment was evidently a rich solution of nutritives, affording unlimited opportunity for exploitation by developing and changing organisms. Assuming this to have been the case, the development of changing forms was greatly encouraged by the environment because there was surely a place in nature for a variety of new organisms.

It is reasonable to assume that up to this point organisms were heterotrophic, simply absorbing nutrients from the environment. Eventually, however, this situation must have changed as the early organic compounds were consumed. Gradually, the victory of survival went to the autotrophs (which had developed synthetic ability) and to the phagotrophs (which consumed other types of organisms as well as one another). Some heterotrophs were able to survive by switching from "natural" nutrients to those provided by these two classes of new organisms, and they were evidently the ancestors of modern heterotrophs. From this point on, it was a matter of further evolution to the present day.

It might be objected that this concept of the origin and early development of life is pure speculation. In consideration of this objection, it should be pointed out that the scientist is often obliged to speculate (hypothesize) in order to approach a problem. If a given hypothesis affords the best explanation possible in terms of the evidence, no matter how fragmentary this evidence may be, the scientist will use it as a working tool. If it becomes reliable in predictability with regard to further investigation, then the speculation, or hypothesis, advances to the status of a theory. Of course, we have no direct evidence that the account given above is strictly and historically correct, but let us remember the nature of scientific theory. *A good theory is one that accounts for more data than any alternate theory.* In this case, most biologists feel that the *theory of origins*

outlined above is the most satisfactory explanation available on the basis of present evidence even though there is some difference of opinion regarding the details.

Regardless of how they account for origins, virtually all biologists of the present day accept evolution as an explanation of the variety of living forms and their various adaptations to particular environments. This is because certain phenomena encountered in nature are meaningful and explicable *only* if the concept of evolution is accepted. In other words, it is impossible to reconcile the data of comparative morphology and physiology, cytogenetics, and geology with strict creationism, unless one completely abandons and ignores the basic assumptions and viewpoints of science. Although we have already considered some of these data in preceding chapters, let us examine aspects of those fields especially pertinent to evolution.

11.2 Some data that support the concept of evolution

As we have stated, evolution is not mere speculation that has been devised in order to avoid the alternative of special creationism. It is true that our knowledge is far from complete as to how and in just what directions the process occurred during various periods of time, but that it did occur is no longer a matter of doubt to most biologists. For purposes of discussion, our knowledge regarding evolution may be classified according to these three subjects: resemblances among present-day organisms, geological evidences of evolution, and operation of genetic mechanisms.

Resemblances among present-day organisms MORPHOLOGICAL RESEMBLANCES There are certain *morphological* resemblances among organisms that indicate genetic kinship. Some of these are very important taxonomically and have been known to biologists for some time. The study of *comparative anatomy* has revealed many striking examples of similarity. For example, the several systems of the vertebrates, including nervous, skeletal, muscular, excretory, and circulatory systems, show a basic similarity with a gradual increase in structural complexity as one proceeds from the agnathans to the mammals. We called attention to the comparative anatomy of nervous systems in this group previously (Figure 9.8), and similar comparisons could be shown for those systems listed and for others. In fact, the study of phylogenetically homologous* organs, illustrated for one

* Homologous organs are those having a similar embryonic origin. Anatomists generally recognize three types of homology as follows. *Phylogenetic* homology is that existing between different species. The arm of man and the wing of a bird, for example, are phylogenetically homologous. *Sexual* homology is that existing between sexes of the same species; the testes of a man and the ovaries of a woman are sexually homologous organs. *Selar* homology is that existing between organs of the same individual that occupy different levels of the body, such as the arm and leg of man.

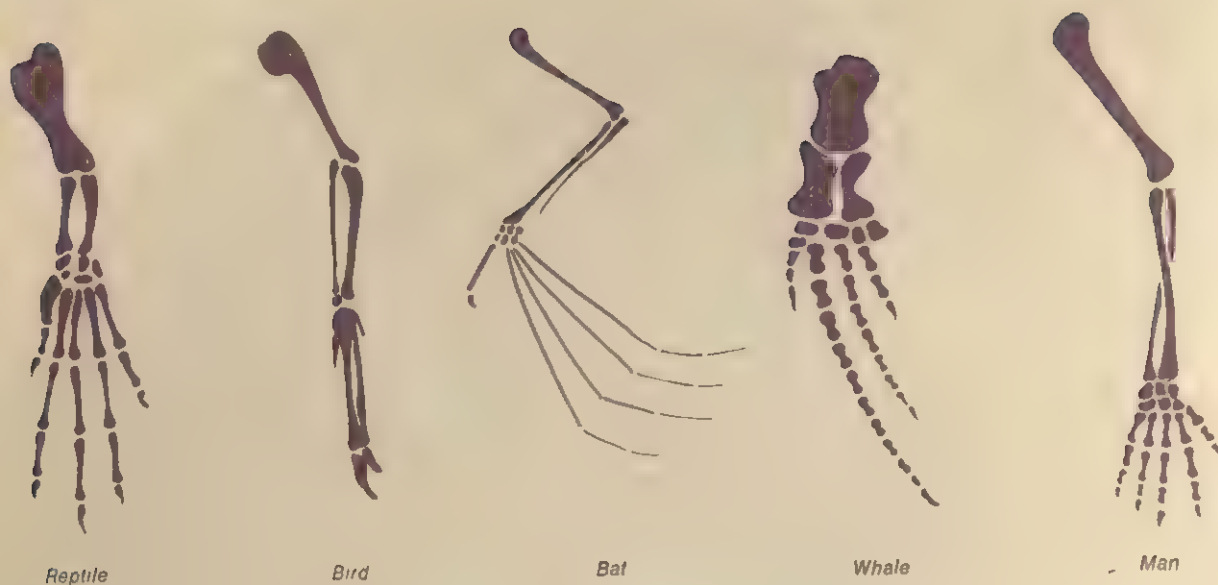


Figure 11.1 A comparison of the forelimbs of various vertebrate animals. Note the general pattern of structure that exists among these homologous organs.

portion of the vertebrate skeleton in Figure 11.1, is very revealing. Upon examination of embryos, it is found that such organs arise in precisely the same manner, indicating that certain gene groups must be shared in common among these animals.

Embryological characteristics are extremely valuable in relating animals in still other ways. The development of a notochord by all chordates, for example, indicates actual genetic kinship among them. Perhaps even more significant is the observation that many organisms develop *vestigial* structures that may disappear during the process of development, or they may persist. All vertebrate embryos, for instance, develop pharyngeal pouches, but these give rise to gills only in the fishes and amphibians. In the reptiles, birds, and mammals, they either disappear or become modified to form other structures. In man, such vestigial structures as the vermiform appendix, the shortened series of tail bones (coccyx), and certain nonfunctional muscles indicate a degeneration of these parts from ancestral groups in which they were functional. Only if such morphological resemblances as these are interpreted according to an evolutionary concept do they become meaningful since creationism is at a loss to explain the significance of such similarities.

PHYSIOLOGICAL RESEMBLANCES There are *physiological* resemblances that are also of significance to our discussion. For example,

certain parasites attack only organisms that bear a close resemblance to each other, and this indicates a similarity in body chemistry. Races of wheat rust, for instance, attack other cereal grains such as barley, rye, and oats, all of which are much like wheat in their external morphology. Undoubtedly, these grains bear a closer evolutionary kinship to each other than to plants that are not attacked by the rust. Among the mammals, endocrine glands and their secretions are sufficiently similar that hormones from one animal may be used to treat deficiency diseases in another. For years, the hormone insulin has been extracted from pancreatic tissue of the sheep and used to alleviate the sufferings of diabetic humans. Apparently, some identical genes exist in the human and other mammals which control the formation and function of the endocrine portion of the pancreas.

Among the most significant of all physiological resemblances (and differences) are those indicated by *comparative serological tests*, that is, the comparison of body fluids according to their respective chemical natures. In vertebrate animals, for example, the introduction of any protein into the blood stream of an animal in which that protein is not found causes a reaction to occur. The foreign protein in this case is called an *antigen*, and it elicits the production of counteracting substances, called *antibodies*, by the affected animal. This phenomenon of antigen-antibody reaction has very important implications for the production of animal diseases, since infectious microorganisms may possess or produce proteins that are antigenic to a host. Many diseases of the human, for example, may be prevented by artificially causing the production of antibodies through vaccination, thus effecting immunization against a given disease. This is made possible through the use of disease organisms that have been killed or modified so that they stimulate production of antibodies without producing the actual disease. For purposes of our present discussion, however, we are interested in antigen-antibody reactions as a tool for determining degrees of genetic kinship.

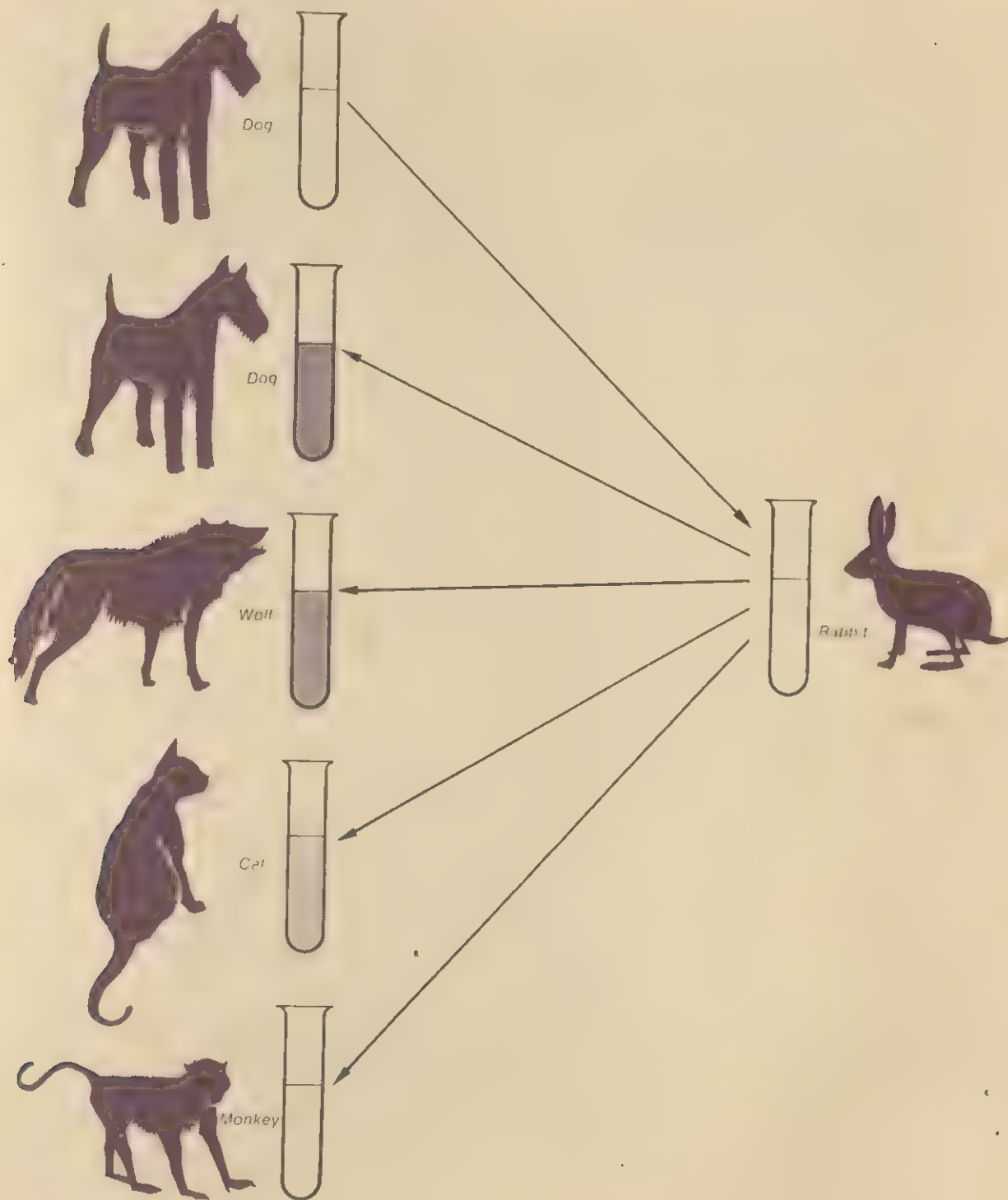
Serological testing reveals that antibodies formed in response to the antigens of a given animal react very strongly with the body fluids of other animals. Significantly, the reaction is strongest in those animals which bear a close morphological resemblance to the animal whose antigens are involved, and it weakens as the degree of morphological resemblance diminishes. In practice, a test is conducted as follows. Let us suppose that we inject some blood from a dog into a rabbit. The rabbit develops antibodies over a period of time which will *precipitate* the foreign proteins (antigens) out of solution. If some of the blood from this rabbit is taken and the serum

is separated from the other components of the blood, it can be used as an antiserum, and reactions can be brought about in test tubes. Upon mixing some of this antiserum (developed in the rabbit) with the sera of other members of the order Carnivora, to which dogs belong, it is found that a gradation of responses occurs. A stronger reaction, shown by a greater degree of precipitation, is seen when the serum of a wolf is mixed with the antiserum than when that of a cat is used, and it is still less severe (or nonexistent) in animals that bear little morphological resemblance to dogs, such as horses or monkeys (Figure 11.2).

In general, serological tests have only verified what was already known from comparative morphology, but there is an extremely important principle here. According to the theory of evolution, morphological and serological resemblances and differences should agree, and this has been the case almost without exception in the hundreds of species that have been tested. Hence, as a working theory regarding the origin of species, evolution is quite satisfactory because it is reliable in prediction. Furthermore, serological testing has been invaluable to taxonomy since it has helped to establish natural relationships among animals, and a variation of it has even been developed for plants. Since genes control protein synthesis, it seems evident that dogs and wolves share more of the same genes than do dogs and cats, for example, since dogs and cats show a greater diversity in their body proteins. Only if it is assumed that these genes had a common origin in the genotype of some remote ancestor do comparative serological tests and their results become meaningful.

CYTOGENETIC RESEMBLANCES It will have occurred to you by this time that degrees of resemblance among organisms depend upon similarities and differences in genotypes. Hence, the morphological and physiological relationships discussed are, in the final analysis, genetic ones. There are certain relationships among organisms, however, that are more fundamentally related to genetics or to cytology than these. For example, the fruit fly *Drosophila* has been extensively studied cytogenetically, and the several species within the genus exhibit some interesting similarities. Some species can be induced to interbreed, with varying degrees of success as to survival and fertility of offspring. Other species will not interbreed under any conditions, even though they may be virtually indistinguishable to the eye. It is significant that when chromosomes from various species of

Figure 11.2 Diagram representing serological testing among animals. See text for amplification.



the genus are stained and observed, they resemble each other very closely; interbreeding species generally show more similarity in this respect than do noninterbreeding ones. It so happens that the chromosomes of these insects can be studied very profitably with regard to the presence of certain visible regions. Interbreeding species are quite similar in the possession of "landmarks" on their chromosomes, whereas those of noninterbreeding species differ markedly. Other cytological and genetic resemblances or differences have been studied closely, and the evidence is overwhelming that these several species share a common ancestry.

On the basis of cytogenetic knowledge, species have actually been "synthesized," which constitutes another example of the validity of evolution as a scientific theory. For example, in 1932 a Swedish geneticist, Arne Muntzing, reported his research in species synthesis using the hemp nettle, *Galeopsis*. He observed that one species, *G. tetrahit*, exhibited sixteen pairs of chromosomes, and that other species possessed eight pairs. Muntzing chose two of these eight-pair species, *G. pubescens* and *G. speciosa*, both of which resemble *G. tetrahit* very closely, and undertook to interbreed them. His efforts were successful, and the resulting offspring were morphologically indistinguishable from the *G. tetrahit* of nature. Thus, he reasoned that *G. tetrahit* had arisen in nature from a cross between the other two species, and that *polyploidy* had been initiated in egg fertilization.* In order to test his hypothesis, he crossed his new species with the natural *G. tetrahit* and found them to be interfertile. Not only was this the case, but their seeds germinated to produce normal *G. tetrahit* plants. That *G. tetrahit* could be called a species, and not a variety, was shown in that neither the naturally occurring type nor the synthetic one could be made to interbreed with either *G. pubescens* or *G. speciosa*. In this fashion, Muntzing actually showed that evolution occurs, and he successfully demonstrated one of the mechanisms by which it comes about.

As is the case with morphological and physiological resemblances among organisms of different species, cytogenetic ones provide very good evidence of close or distant relationships. Unless evolu-

* Polyploidy may be defined as the multiplication of whole "sets" of chromosomes. The establishment of polyploid races or species sometimes occurs in plants, but only rarely in animals. The most common method in nature seems to be that gametes from two plants that are members of different but closely related species fuse successfully, with each haploid "set" of chromosomes subsequently undergoing duplication. Polyploidy is fairly readily induced in many cultivated plants by the use of certain techniques, and it seems to occur often in nature. It is a very useful phenomenon, frequently resulting in varieties or species of cultivated plants which are more productive than ordinary diploid ones. All commercially valuable varieties of wheat, for example, are polyploids.



Figure 11.3 Fossil animals (a) an insect, (b) a fish. These fossils are probably about 50 million years old. (General Biological Supply House, Inc.)

tion did occur, such resemblances or differences are meaningless.

Geological evidences of evolution Geology, which is the study of the earth and its history, provides a great many clues to the process of evolution. In fact, of all the natural phenomena which indicate that such a process has occurred, those which are geological in nature are perhaps the most convincing. We shall call attention to some of the most important of these phenomena.

THE FOSSIL RECORD When organisms die, their bodies decompose under most conditions within a relatively short space of time, and no trace of them remains. There are some exceptions to this rule, however. They may be preserved entirely or in part by some means, or *imprints* of the organism may be preserved. Such *fossils* (Figure 11.3) are the materials of that joint field of biology and geology known as *paleontology*, and although relatively few plants and animals leave any sort of fossil record, sufficient kinds and numbers have been found and studied to lend considerable support to the view that evolution has occurred.

In the past, many living forms have died under such conditions that their bodies became covered with various sediments. Where the exclusion of oxygen was sufficiently complete as to prevent decay, a given organism would be entombed and fossilized. As layer after layer of deposited material covered the organism, with other organisms being fossilized in each succeeding layer, a fairly accurate record of living forms belonging to the region, over time, was established. By digging down through successive strata of deposits in a great many different areas, paleontologists have been able to gain a fair impression of the fossil record.

As might be expected, there is a general trend toward structural simplicity of fossil organisms as one proceeds from the surface of a deposit to greater depths. Among animal fossils, for example, only invertebrates appear in the lowest and most ancient strata. These are followed by primitive fish-like vertebrates, then by true fishes, and eventually by amphibians and reptiles. Birds and mammals are the last to appear, and in the youngest strata, fossilized representatives of these two groups resemble present-day forms more than do the earlier ones. Similarly, fossilized plants show a definite pattern in the correlation of complexity and order of appearance. In spite of the incompleteness of the fossil record, since some organisms did not lend themselves readily to fossilization, enough has been discovered to establish general evolutionary trends.

THE ESTIMATION OF TIME How, it might be asked, can geologists establish time scales whereby it may be known that various fossil organisms lived during certain ages? This is a very important question mostly because no one location on earth has been found to contain strata representing all geological periods, and comparisons must be made in order to establish a consistent pattern. Of the several factors that are indicative of geological time, the following are outstanding. At least, they should serve to satisfy the student that geologists have not merely guessed at the matter.

One class of rocks, the *sedimentary* rocks, are formed by the accumulation of eroded materials and various sediments. On the basis of time measurements, present rates of sedimentary rock formation are known rather accurately. If it is assumed that rates of sedimentation have always been about the same, then, some estimation of ages of sedimentary rock deposits (which often contain fossils) may be made. Unfortunately for the accuracy of this method, it is not certain that these rates have always been the same. In a comparative way, however, by establishing relationships between strata of different areas, this method of dating is quite valuable. Consequently, it provides a rough indication of just how long ago a given fossil became entombed. By this means, it has been possible to determine with some accuracy the age of any given stratum of sedimentary rock and to relate it to a comparable stratum. At the very least, *relative* ages of fossil organisms may be established.

Early in the present century, a more accurate method of dating materials was developed. This is called the *uranium-lead method*, and it is useful because uranium, which is a radioactive element,* disintegrates at a constant rate to form lead and helium. Precise determinations have indicated that through such spontaneous

* A radioactive element is one whose atomic nuclei are unstable, disintegrating at a certain rate to form stable elements of less complex atomic structure.

decomposition a given deposit of uranium loses half its radioactivity in about 4.5 million years. This loss is accounted for by the presence of a certain quantity of lead. Since the rate of lead formation under these circumstances is thus known, the age of a rock can be determined rather accurately by comparing the weights of uranium and lead which are present in the rock. Fortunately for the accuracy of this method, a newly crystallized rock contains only uranium, no lead from previous disintegration, and the time that the rock was originally formed may thus be determined. Now let us suppose that a fossil organism is present in a rock located within a stratum that can be dated by the uranium-lead method. This means that it was trapped within the rock at the same time as the uranium, and its age is thus determinable.

Unfortunately, uranium is relatively rare, and those rocks we would like most to date seldom contain it. However, the uranium-lead method has proved to be highly valuable, particularly in telling us something of the age of the earth and of the probable time that life has existed upon it. Furthermore, methods of dating have been developed that depend upon other radioactive elements than uranium. (For example, a potassium-argon "radioactive clock" has been developed that is suitable for dating fossils that are several million years old.) One of the most useful procedures is the *radiocarbon method*. It depends upon the well-substantiated theory that of the carbon utilized by organisms, a small but constant proportion is radioactive (${}^{14}_6\text{C}$). Determinations indicate that a given quantity of radioactive carbon loses half its radioactivity in about 5,760 years. This means that materials such as bone, leather, or wood, which at one time were a part of a living organism, can be analyzed for the amount of radioactive carbon present. This may be compared with the amount present in a *fresh* piece of similar material, and the age of the test piece can be determined by computation. This method is highly accurate, since tests involving materials of known age, such as manuscripts written on animal skins, show that estimated age agrees very closely with known age.

The accuracy of the radiocarbon method is limited, unfortunately, to materials that are no more than about 40,000 years old. Nevertheless, it has proved to be quite valuable in dating fossils of recent periods of time, and doubtless its applicability to paleontological problems will eventually be increased. Thus far, it has been extremely valuable in solving a number of archeological problems regarding the ages of certain civilizations and in determining the ages of recently fossilized organisms.

On the basis of all methods of estimating geological time, there is little doubt that evolution has occurred over a period of many mil-

lions of years. In fact, paleontologists are fairly certain of the periods of time that various organisms first appeared on earth and when some of them vanished. Table 11.1 summarizes estimates that are now generally accepted as being reasonably accurate ones.

Operation of genetic mechanisms We called attention in a previous topic to the cytogenetic resemblances that frequently exist among closely related organisms and to species synthesis. Such lines of work were initiated when the knowledge of genetic mechanisms was sufficient to enable biologists to make predictions regarding these and other evolutionary phenomena. Within the past few decades, our knowledge of genetic mechanisms has expanded so rapidly that it ranks with the older comparative and geological studies in supporting the concept of evolution.

Since we reviewed elementary principles of genetics in Section 8.6 and because we shall relate these and other genetic principles to evolution in the following section, it will be sufficient at this point to observe the relationship between our knowledge of genetic mechanisms and the concept of evolution. In many cases, this knowledge enables us to interpret certain data meaningfully, and in others it provides a basis for the formulation of theories with which to work. To say the very least, genetic mechanisms achieve their greatest significance within a conceptual framework of evolution; and, in turn, evolution takes on an added dimension when it is related to genetic mechanisms.

11.3 Processes of evolution We have pointed out that evolution is subject to consideration as a concept, as a theory, or as a process. So far we have devoted some attention to all these aspects of evolution except the last one. As a concept, or viewpoint of nature, an evolutionary interpretation is a virtual necessity for a person who is aware of even a small part of the biological knowledge available. As a theory or conceptual scheme, evolution has been quite fruitful, and has led to other conceptual schemes which were not attainable in any other way. As a process, evolution is probably as firmly established as can be expected of any series of historical events not susceptible to direct witness. The millions of years which have elapsed during the course of evolution make it among the most difficult of historical subjects to study.

Admittedly, these three aspects of evolution are not easy to understand or appreciate without a considerable amount of study and thought. Nevertheless, evolution as a process is the most difficult of all to grasp, and perhaps the most important to an understanding of biology. For this reason, we shall devote special attention to it. As is the case with any difficult subject, it is helpful to trace

Table 11.1 *Geologic time, the earth, and the rise of living forms*

Era	Period	Time*	Environmental conditions	Biotic development
Cenozoic	Quaternary	1	Successive ice ages; after last one (25,000 years ago), climate warmer	Man and other placental mammals dominate scene; many plants and animals become extinct.
	Tertiary	65	Rise of Alps and Himalaya; climate growing colder.	Man evolves; mammals become dominant animals; forests become widespread.
Mesozoic	Cretaceous	135	Rise of Rockies and Andes; inland swamps common.	Dinosaurs flourish and become extinct; gymnosperms decline.
	Jurassic	195	Continents high and small, much of present area submerged under sea.	Rise of marsupial mammals; rise of angiosperms from gymnosperms.
	Triassic	225	Great desert areas prevail.	Rise of dinosaurs, birds, and egg-laying mammals; gymnosperms dominant plants.
Paleozoic	Permian	280	Rise of mountains; glaciers and deserts common.	Rise of mammal-like reptiles; decline of dominant fernlike plants.
	Carboniferous	345	Climate warm and humid, becoming cooler; coal deposits formed	Rise of reptiles; fernlike plants and gymnosperms form great forests.
	Devonian	395	Inland seas grow smaller; glaciers and deserts form.	Rise of amphibians; first vascular plants; fishes widespread.
	Silurian	435	Rise of large land areas with great inland seas; continental seas large.	Rise of insects; fish species become very numerous; algae are dominant plants.
	Ordovician	500	Land extensively submerged; climate very warm over entire earth.	Rise of fishes; many species of invertebrates widespread; rise of land plants.
	Cambrian	570	Lands very low; climate mild.	Rise of primitive vertebrates and protochordates; algae widespread.
Pre-Cambrian†		1,000	Extremely violent conditions, involving volcanos, glaciers, and * unstable atmospheric conditions.	Rise of algae, fungi, and modern invertebrates.
		3,000(?)		No fossil record: It is assumed that first living forms developed less than 3 billion years ago.

*Estimated in millions of years measured from the beginning of the period or era to the present

†The term Pre-Cambrian is not used by geologists to represent an era, it simply denotes time that existed previous to the Cambrian period. Although the universe is probably some 5 billion years old or more, Pre-Cambrian time is usually considered that which began about 3 billion years ago.

its development, so let us begin with an examination of the earliest ideas on the subject and trace them to the present time.

The history of evolutionary thought THE PERIOD OF SPECULATION There have probably been evolutionists ever since man first contemplated nature, but ancient Greeks were the first to express the idea that some forms of life may have sprung from other forms. As was characteristic of much of their thinking about natural phenomena, the good and the bad were so interwoven that most of it must be put down as hopeless and fruitless speculation. There was no improvement in evolutionary thinking until the eighteenth century, when the French biologist Comte de Buffon and the English naturalist Erasmus Darwin advanced their ideas that species of organisms are not immutable or unchanging. The times were such that considerable stimulus was afforded the speculative mind, the work of Linnæus, for example, focused attention on species as entities in nature which deserved some explanation. However, there were also good reasons why evolutionary thinking was not likely to be met with enthusiasm during the eighteenth century, and the ideas of Buffon and Darwin found little acceptance. Their cause was not helped by their inability to show little more to substantiate their speculations than their own fertile imaginations.

More significantly, the French biologist Jean Baptiste Lamarck (1744–1829) set forth a hypothesis of evolution in the early nineteenth century which attracted serious attention from some biologists of that period. Essentially, Lamarck's idea was that species change through the use and disuse of parts. He supposed that the continual use of a body structure by an organism would strengthen and perhaps enlarge the structure and that this modification would then be inherited. For instance (and this is the most frequently cited of Lamarck's examples), he speculated that giraffes originally had short necks, but through stretching to reach higher leaves, their necks became longer. This process would explain such adaptations as the long ears of rabbits, the wings of birds, and the claws of tigers. Known today as the *theory of inheritance of acquired characteristics*, Lamarck's hypothesis is unacceptable to modern biologists. However, it must be remembered that it was almost a century after Lamarck that genes and their role in inheritance were known, and it is worthy of note that any biologist of that period would express a belief in evolution and attempt an explanation of the forces responsible for it. Although his was an inadequate explanation, Lamarck did much to focus the attention of other biologists upon the problem.

CHARLES DARWIN AND NATURAL SELECTION In addition to the stimulus to evolutionary thought provided by Lamarck (although his explanations were generally rejected), some exciting discoveries were being

made in geology during the early part of the nineteenth century which bore upon the subject. New methods were developed for estimating the ages of rock and soil formations, and it was determined that the earth was far older than had been generally supposed. Furthermore, it was shown through the study of fossils that organisms had existed long before the time set by special creationists of the period for their origin. Evolution was staring biologists and geologists in the face, but no one at that time took advantage of the opportunity to explain the new findings in terms of this concept.

It remained for the English naturalist Charles Darwin (1809 - 1882), grandson of Erasmus Darwin, to gather and interpret the data according to an evolutionary viewpoint. Actually, he started thinking about evolution while he was on a voyage of exploration lasting from 1831 to 1836. His observations convinced him that species were not immutable, and he began to search for explanations as to how evolution might occur. He thought carefully and deliberately about the problem for more than twenty years before publishing his views. Finally, in 1859, his book appeared under the title *On the Origin of Species by Means of Natural Selection* and created an immediate sensation. In fact, it eventually became established as one of the most important books of all time because of its profound influence upon human thought.

In *The Origin of Species* (the title's usual abbreviation), Darwin set forth the view that evolution has occurred, and he attempted to explain how it occurred. He called his explanation *natural selection*, and in setting it forth, he emphasized the following observable phenomena:

1. Variation exists within species (that is, no two individuals are exactly alike).
2. Overproduction of offspring is characteristic of organisms.

Although these statements are self-evident to any person who has made even elementary observations of plants and animals, Darwin justified and reinforced them with numerous examples. After he felt that he had firmly established their validity, he proceeded to draw two logical conclusions:

1. Of the varying individuals in a given group of organisms, the less fit do not survive; thus, nature "selects" the more fit, which live to reproduce.
2. Favorable traits for survival are passed on from parents to offspring.

Of these two conclusions, the first was by far the easier to approach, and Darwin emphasized it very strongly, presenting quantities of data which indicated its general validity. The second conclusion was never verified by Darwin (remember, the science of genetics

had not yet been developed), and his attempts to explain it eventually led him into difficulties. As a matter of fact, Darwin's genetic hypothesis was essentially Lamarckian in that it assumed an influence by ordinary body cells upon those involved in sexual reproduction.

Another difficulty inherent in natural selection as Darwin expressed it was that it seemed to operate as a limiting factor, determining in what direction evolution could or could not go, but it did not explain the origin of such phenotypes as natural selection might influence. Darwin used such expressions as "struggle for existence" and "survival of the fittest," which implied that natural selection is chiefly a process that operates to eliminate the unfit. His critics pointed out, with some justification, that natural selection was simply a negative factor in evolution, and that Darwin's theory essentially said that unless organisms can compete successfully, they do not survive. As we shall see, this negative aspect of natural selection is indeed only part of the story, and it also required genetic insights in order to become more than a rule governing the elimination of the unfit.

In summary, Darwin made two outstanding contributions to evolutionary thought. The first of these was his establishment (on a valid historical basis) of evolution as a *process*. Evidence that has been found since his time has only strengthened Darwin's case, but he was able to present enough data to convince all but the most skeptical in his day that evolution had indeed occurred. His second contribution was his identification of natural selection as an important factor in adaptation and the origin of species. As we pointed out, Darwin lacked the genetic insights necessary to a clear exposition of natural selection—and there were other difficulties as well—but it is a tribute to his genius that his concept of the processes of evolution was essentially a clear one.

THE RISE OF GENETICS AND THE MUTATION THEORY The period between 1859 and 1900 was a time of rapid development in biology. Mendel's work was published in 1866, chromosomes and their behavior in mitosis and meiosis were described between 1866 and 1885, and rapid progress was evident in virtually every area of biology. Nevertheless, the fundamental principles of genetics had not been clarified (Mendel, you will recall, had made no impact on the scientific world). In 1900, Mendel's work was rediscovered by three biologists working independently, which is an indication that the time was ripe for its understanding and appreciation.

Strangely enough, the new science of genetics appeared at first to be devastating to Darwin's theory of natural selection. This was partly a reflection of the human tendency to view a new piece of knowledge as the whole truth (scientists are not immune to this fallacy), and partly a misunderstanding of the raw materials of both

genetics and natural selection. Specifically, the conflict arose when the process of *mutation* was discovered shortly after Mendel's paper was found. Today, we define mutation as a change in a gene (or biochemically speaking, an alteration of nucleotide sequence in a specific region of a DNA molecule)*, but it was first looked upon as an almost mystical force which could effect profound changes in hereditary materials. Because certain observations were made involving gross chromosomal abnormalities which appeared to create new species in great and sudden jumps, an alternative hypothesis to natural selection was put forth. Called the *mutation theory*, it soon claimed large numbers of leading biologists among its adherents. It was not until the 1930's that mutation and natural selection were reconciled and, in the meantime, Darwin's views were generally regarded as being badly outmoded.

As it turned out, the mutation hypothesis revealed itself as one of those half-truths which look better at first inspection than they do after they have been subjected to experimental analysis. Mutation is indeed a major factor in evolution, as we shall emphasize presently, but not in the sense conceived by early champions of the mutation hypothesis. They visualized mutation as a process which resulted in sudden and drastic improvements in organisms, and to them, natural selection was merely a negative factor which eliminated the unfit. It was subsequently shown that the vast majority of mutations do not produce drastic changes in organisms—and when they do, the affected organisms are almost always unable to compete with the standard types from which they mutated. Several years were required to obtain a better understanding of the nature of mutation as a process, and several years more passed before these earlier misleading concepts were overcome.

THE MODERN SYNTHESIS Shortly before and during the 1930's, the major factors of evolution began gradually to fall into place. By this time, both mutation and natural selection had been subjected to considerable study, and other factors appeared to be involved in evolution besides these two. One of the most important developments was the introduction of statistical methods into genetics, and once large numbers of organisms could be analyzed to determine how evolution actually worked, it became much easier to fit the pieces of the puzzle together. Since that time, the *synthetic theory* of evolution has replaced the older hypotheses, and the feeling among most modern biologists is that no additional basic factors of evolu-

* Technically, the term mutation applies to gross changes in chromosomes as well as changes which occur in genes. From this viewpoint, a distinction is made between *genic* or *point* mutations and *chromosomal* mutations. We shall use the term to include only genic mutations.

tion remain to be discovered. This does not mean that everything is known about evolution as a process; it simply means that no data have been forthcoming for several decades which cannot be accommodated by the synthetic theory, and that it attains to an exceedingly high degree of reliability in prediction.

The major factors of evolution We call the modern theory of evolution a synthesis because it incorporates and unifies the several factors which are known to be operative in effecting changes among organisms. Included are natural selection and mutation which, as we have seen, were each championed at one time as being self-sufficient to explain the process of evolution. Not only are other factors now recognized, but each is related to the others in such a way that the total picture is meaningful. We shall attempt to devote some attention to these factors as they relate to the whole of evolution.

The synthetic theory of evolution recognizes four basic processes. Two of these, mutation and genetic recombination, are the sources of evolutionary variability. The other two, natural selection and reproductive isolation, act upon the sources of variability in determining adaptation. We shall discuss these factors in turn.

MUTATION Since Darwin's time, the phenomenon of mutation has been discovered and studied extensively. A mutation is a change in a gene, and although genes are highly stable, usually duplicating themselves with fine exactness, every now and then a mutation does occur. This may be due to some fault of genic reproduction; für example, the "wrong" nucleotide may somehow be substituted for the original one somewhere in the gene. Another explanation for mutation is that a chance "hit" on some portion of the gene by a high-energy radiation particle may cause a chemical change. Experimentally, mutation rates may be increased many times over by the use of radiation. At any rate, genes are not completely stable, and when a gene mutates, its new form is duplicated in cell division as was the old one.

If a mutation occurs in an organism without affecting its reproductive cells or its reproductive potential, there is neither genetic nor evolutionary significance to the event. Any resulting changes spread no farther than such cells as may be produced from this cell, and effects are thus localized. In other words, the mutation, whether potentially advantageous or detrimental to the organism, is of necessity lost to the species when its bearer dies. However, if a mutation occurs in a reproductive cell which becomes involved in the formation of a new individual, there is a chance that it may produce significant effects in the species. It so happens that most mutations are harmful ones; a mutant gene may change the smooth balance of factors concerned with development so radically, for example, that

the bearer does not even survive until birth. In other instances, mutant genes may be responsible for structural or functional abnormalities in the fully formed individual.* It should not be difficult to see why most mutations are harmful; after all, the thousands of genes that contribute to the genetic make-up of a complex organism are of necessity highly coordinated. Over long periods of time, the species of which it is a member has adjusted to its environment and is obviously successful to some degree, or it would be extinct. The chances are considerably greater that a random mutation will upset this genetic balance rather than improve upon it. To draw an analogy, it is possible that one might improve the operation of a highly organized machine by throwing a heavy wrench into its gears, but the chances are much greater that such action will only succeed in tearing up the machine.

Nevertheless, an advantageous mutation does sometimes appear in species, and when this occurs, there is a chance that it may become a part of the stable genotype through the process of natural selection. Thus, over long periods of time, species may change for the better in terms of ecological success through the accumulation of advantageous mutations.

As related to the other factors of evolution discussed below, mutation is the *primary* source of genetic variability, or the raw material with which the other factors have to work. Apparently, it is the only mechanism by which new hereditary material is incorporated into genetic systems.

GENETIC RECOMBINATION In sexual reproduction, different gene combinations may be brought together in the formation of a new genotype. Any differences in allelic genes depend ultimately upon mutation, of course, but for the new organism, its gene pattern is a result of the new combinations brought about through sexual reproduction. We call this phenomenon *recombination*, and it may be defined as the production of new genotypes from genes which already exist. By its nature, therefore, recombination is a *secondary* source of genetic variability.

Recombination occurs in three different ways. (1) When a set of chromosomes from one parent becomes associated with a set from the other parent in sexual reproduction, many new combinations of

* Of course, if the "new" gene were recessive to its normal allele, as most mutant genes apparently are, it would be carried in the heterozygous condition and would not appear until a combination of two such genes occurred (see the discussion of recombination below). Because there is a good chance that any given human gamete may carry a harmful recessive mutation, laws forbidding the marriage of two persons who are closely related are genetically sound since this provides a better opportunity for two recessives originating in a common ancestor to come together in the homozygous condition.

alleles are made possible in the diploid zygote. Ultimately, these may be expressed in the total genotype of the organism. (2) During meiosis, the formation of chiasmata between chromatids of homologous chromosomes may result in a new combination of genes for each chromatid involved. (3) Also during meiosis, chromosome "sets" may become changed in number, or individual chromosomes may undergo changes.

In listing these methods of recombination, our discussion seems oriented toward diploid organisms, which raises an interesting point. You are aware, of course, that the vast majority of species are characterized by diploidy, and you will probably have no difficulty in seeing how recombination operates when chromosomes exist in pairs. Actually, haploid organisms that reproduce sexually at least some of the time (this includes most of them) may experience changed genotypes through recombination. This is because new combinations of chromosomes may be incorporated into new individuals, which is somewhat analogous to the shuffling of cards in a new deal, or chiasma formation may be responsible for new combinations within a given chromosome. Nevertheless, evolution has definitely "favored" the diploid condition (Figure 11.4). Perhaps we can understand why after we have reflected a little on the circumstances.

You will recall our statement that most mutations are harmful to

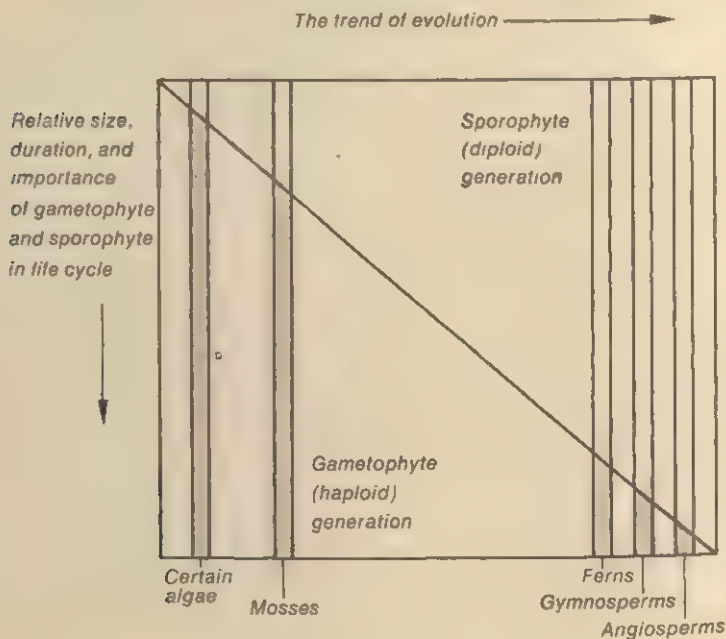


Figure 11.4 The evolutionary history of plants shows particularly clearly how the emphasis has shifted in the life cycle from gametophyte to sporophyte (haploid to diploid). This, among other lines of evidence, suggests that diploid organisms or phases of life cycles have certain evolutionary advantages over haploid organisms or phases of life cycles.

the organism in their expression, and most are apparently recessive. In a diploid organism, any new mutant gene involved in recombination is "covered" by its dominant allele on the homologous chromosome. Consequently, several generations of inbreeding might be required before recombination produced a homozygous genotype for any particular recessive mutant. For this reason, diploid organisms have a built-in protection against harmful mutations, and they may carry numerous genes which, if they were expressed in the homozygous condition, would reduce their vitality or even kill them. As a matter of fact, it has been estimated that most complex organisms, which carry perhaps 10,000 genes or more in their total genotype, probably have a number of such potentially harmful genes. Haploid organisms obviously have no such advantage. Any mutant gene is *immediately* subject to natural selection. To draw an analogy, haploid organisms are obliged to pay cash for their "mistakes" (mutations), while diploid organisms are able to pay on the installment plan.

Apparently it is not by accident that the majority of organisms in nature are diploid, since the diploid condition gives an organism quite an advantage in absorbing potentially harmful mutant genes. You may wonder why haploid organisms have not disappeared completely. There is a possible explanation for this, but it would take us beyond the scope of this book. Suffice it to say that diploidy is characteristic of most species at the present time, and it is within diploid genetic systems that recombination works most effectively as an evolutionary factor.

The third type of recombination we have listed, changes in chromosomes, is a very important secondary source of genetic variability. In order to understand the nature and significance of this factor, we must first "unlearn" a biological principle. We observed in an earlier chapter that the number and individual form of chromosomes in body cells is the same for all members of a given species. Called the *chromosome number law* when formulated around the turn of the century, this principle appeared at first to be an argument against the very occurrence of evolution. However, subsequent investigation revealed that violations of this law are not infrequent in nature, and indeed, that they constitute a very important source of genetic variability.

Chromosomes may lose entire pieces of chromatin, and any gametes carrying such a deficient chromosome may exert profound and far-reaching effects upon the species involved. Again, chromosomes sometimes pick up extra pieces of chromatin lost by other chromosomes, with similar potentially far-reaching effects. Still another type of chromosomal change occurs when a portion of the

chromosome becomes inverted, or switched from its original position. Or further, nonhomologous chromosomes sometimes become entangled and exchange pieces of chromatin. All of these chromosomal changes cause rearrangements in genic materials, with the result that variability is produced. We mentioned the extensive work that has been done with *Drosophila*, a genus of flies, when we discussed the evidences of evolution (Section 11.2). Detailed studies of chromosomal morphology in this genus indicate that such chromosomal changes as we have listed were very much involved as a source of genetic variability in the evolution of the various species.

In addition to those changes which affect individual chromosomes, there may be variations in the chromosome *number* of individuals within a species. Again, this is initiated when a chromosome is lost or gained during a divisional process, and if a gamete which receives an abnormal set of chromosomes becomes involved in fertilization, the event may have evolutionary significance. Changes in chromosome number may be responsible for "immediate" evolution (in plants, at least) through polyploidy. Changes in number of chromosomes are apparently not so important in evolution as the changes in form discussed above.

NATURAL SELECTION Given the sources of variability which we have discussed, it is important that we see how they concern organisms and species as they actually exist in nature. We mentioned earlier that two factors—natural selection and reproductive isolation—operate to influence the adaptations of organisms, and we shall attempt to clarify these processes.

Darwin conceived of natural selection as an essentially negative force in evolution, serving to eliminate those organisms and species which could not compete successfully with other organisms and species. It would be unfair to imply that Darwin's outlook was entirely negative: as he saw natural selection, it allowed superior organisms and species to succeed when those which were less fit perished. Furthermore, it would be grossly unfair to imply that since Darwin could not explain heredity, he could not be trusted to explain anything else. This was a prevalent attitude among the early adherents of the mutation theory, and a trace of it remains in biology even today. That Darwin was a genius should be clear to anyone who has read *The Origin of Species*, and his theory of natural selection was the first attempt to explain evolution that really made sense. It still makes a great deal of sense, and subsequent developments have generally served to clarify and expand Darwin's theory, not invalidate it. As a consequence, we mean the same thing today that Darwin meant when he used the term natural selection, but we mean some additional things as well.

Perhaps the most direct way to define natural selection in the modern sense is to say that it is *differential reproduction*. In other words, organisms with inferior traits leave fewer offspring than do those with superior traits, on the average. "inferior" and "superior" being defined by the environment. By its very nature, natural selection does not initiate these traits; this is the role of mutation and recombination. Furthermore, environment plays only a limiting role in natural selection (and it is here that the modern definition differs most from Darwinian definition); it plays no part in producing variations, but it serves as the ultimate test for the "fitness" of variations. Those organisms which survive reproduce, and their genes are passed on to their offspring. Those organisms which perish do not reproduce at all, or else they produce fewer offspring. Adaptations arise, therefore, whenever they bestow some advantage upon their possessors against which less fortunate organisms are unable to compete, *within the stated environment*.

Perhaps this seems like a very straightforward and simple process, and it even appears to make good sense. We might do well, however, to remember the advice of Alfred North Whitehead: "Seek simplicity — and distrust it." As it actually occurs, natural selection is not at all simple. It is a very complex affair, and it requires special techniques and statistical tools for its analysis. Those studies which have substantiated natural selection as a process in evolution are exceedingly intricate, and we shall not attempt to review them at this point. However, in a later section we shall look at some examples of evolution in which natural selection has played an obvious part, and perhaps its role will be somewhat clearer when it is viewed in relation to other factors.

REPRODUCTIVE ISOLATION Every student of nature is well aware that species are not distinct and readily identifiable entities. Complex interactions of organisms, including the tendency of animals to move about, result in a heterogeneous mixture of individuals belonging to a variety of species. There are very few environments where only one species is found.

A close analysis of any given species reveals that it is usually composed of different *races*, that is, types which differ from each other in various ways, but which may still interbreed rather freely with the production of fertile offspring. For example, thirteen races of the garter snake *Thamnophis elegans* have been recognized, and each race generally occupies a different geographical area. Theoretically, whenever two races become geographically isolated to the extent that they interbreed only within an overlapping area, they are called subspecies. In turn, if a subspecies becomes absolutely isolated from other subspecies in a reproductive sense, it is called a

The concept of evolution

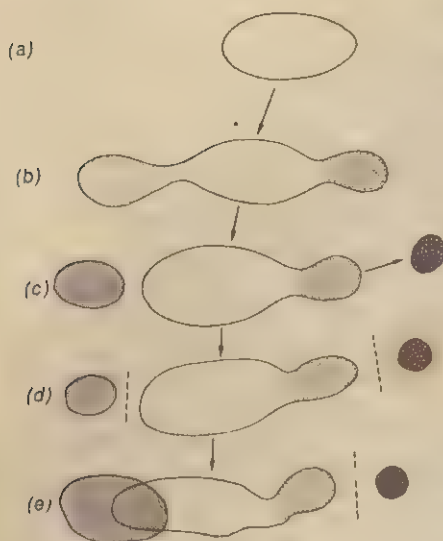


Figure 11.5 Diagram showing the sequence of events leading to the production of different races, subspecies and species, starting with a homogeneous, similar group of populations. (a) A single population in a homogeneous environment (b) Environmental differentiation and migration to new environments produce racial differentiation of races and subspecies (indicated by different shadings). (c) Further differentiation and migration produce geographic isolation of some races and subspecies. (d) Some isolated subspecies differentiate with respect to genic and chromosomal changes controlling reproductive isolating mechanisms. (e) Environmental changes permit once-isolated populations to exist in the same region, now remaining distinct because of the reproductive isolating barriers that separate them; they can be recognized as good species. (From Stebbins.)

species. In practice, it is very difficult to recognize whether or not a population of organisms constitutes a race, a subspecies, or a species. Nevertheless, these distinctions are quite valid, and we can discuss the problem of species formation within the framework of the definitions given.

On the basis of those researches which have been carried out, and they are many, it appears that new species originate by small steps whenever isolated populations become races, when the races become subspecies, and when the subspecies become species (Figure 11.5). By using the expression "isolated," we are speaking in terms of any mechanism that prevents any two groups within a species from interbreeding.

In geographic isolation, populations may be separated by water or land barriers and thus go their separate evolutionary ways. Mutation and recombination occur differently in each group, and natural selection acts, in each case, on whatever is produced through variability. If the environments are similar, there may be no actual reproductive isolation, even though the populations are separated for long periods of time (millions of years, apparently, in some cases). Frequently, however, chance mutations and recombinations acted upon by natural selection create differences of such magnitude in the populations that they will not interbreed if they are brought back together. We called attention previously to the fact that several degrees of reproductive isolation have occurred in *Drosophila*.

Organisms may be genetically isolated through variability within a population. For example, many animals exhibit highly intricate courtship patterns which depend upon precise stimulus-response mechanisms, and even a single mutation may alter this pattern sufficiently in a given organism that it will be less likely to participate in reproduction. In many cases, this would simply mean that natural selection "discriminates" against this set of genes to the extent that it soon disappears. It is possible, however, for such a mutant gene to become fixed in the population sufficiently that it gives rise to a new race. This is only one of the many ways in which genetic isolation can occur; different modes of sexual reproduction and different expressions of the environment make possible the existence of a great variety of such isolating mechanisms.

It should be noted that reproductive isolation resulting in the rise of a race (incipient genetic isolation), then a subspecies (partial genetic isolation), and then a species (complete genetic isolation) may take a tremendously long time. It has been estimated that, on the average, establishment of a new species in nature by this route takes something like a million years. It is small wonder that many people fail to grasp or to appreciate the process of evolution.

Perhaps we are in position now to formulate a better definition of the term "species" on the basis of genetic and evolutionary concepts than we supplied tentatively in Chapter 4. At least among sexually reproducing organisms, we can say that a *species is a group of similar organisms which are actually or potentially capable of successful interbreeding with the production of fertile offspring*. However, it must be remembered that it is rather difficult to determine the exact point at which a race becomes a subspecies, or just when a subspecies becomes a species. For this reason, students of speciation and evolution constantly face a great many problems both in their studies of natural groupings and in their agreement on definitions at all levels.

11.4 Evolution and adaptation Now that we have some basis for understanding the origin of adaptations and of species, let us return to a consideration of adaptation as a process. The end result of evolutionary change is the production of organisms which are better adapted to their environment than any which may not have survived competition with these forms. Consequently, adaptation is one aspect or facet of evolution. To put the matter another way, evolution results in adaptation, but it also results in changes which are *not* adaptational. It has been estimated, for example, that fewer than one-tenth of the number of species that ever existed are extant today. This means that some nonadaptation has occurred along the way (although many now-extinct organisms such as the dinosaurs were spectacularly successful at one time). When we consider that the figure of one-tenth is a conservative one, and it does not take into consideration the myriads of subspecies and races which must have been eliminated over the years, the difference between adaptation and evolution becomes quite apparent. To summarize, all adaptation is evolution, but not all evolution is adaptation.

Although it is extremely difficult to trace the evolutionary development of any given adaptation because of the time element involved and the scarcity of good materials with which to work, we can make some short-term observations which are fruitful. By extension, we can then assume that similar processes have been operative during the course of evolution. To illustrate, let us consider a study of adaptation conducted in England over a period of years. This case will also provide us with some insight into the role of natural selection in evolution.

Over a hundred years ago, insect collectors observed that certain species of moths existed in England as light and dark forms. At that time, the overwhelming majority of individuals in a given species were light; dark forms constituted fewer than 1 percent of the total

population, and were considered to be "sports" or curiosities by insect collectors. These proportions were found in areas of England which had not been industrialized at that time. Several decades later, these same areas were industrialized, and it has subsequently been found that up to 90 percent of the moths belonging to a given species are dark in those areas.

Theoretically, the explanation for this phenomenon is quite simple. Moths often rest on the trunks of trees in daytime. As long as no industries occupied these areas, the trees were covered with lichens. Moths which are light in color blend very nicely with lichens, and are thus protected from their enemies (for example, birds). Fumes and soot from industrial plants killed the lichens in the areas under consideration, however, and many of the trees became blackened by soot deposits. Light forms were now at a considerable disadvantage when resting on such tree trunks, whereas dark forms were favored. Consequently, the victory of survival swung in the direction of dark forms. Let us note that this explanation fits the synthetic theory of evolution, but simply observing and explaining the phenomenon in this manner does not bear out this theory; it merely assumes it.

In order to test this apparent case of natural selection, the English biologist H. B. D. Kettlewell carried out a series of studies, beginning in the 1950's, on light and dark forms of the peppered moth, *Biston betularia*, shown in Figure 11.6. In this study, light and dark forms were released in an industrial area (Birmingham) and in a nonindustrialized area (Dorsetshire). By using ingenious photographic methods, and by careful and painstaking observation, Kettlewell substantiated the expectation that natural selection was indeed operative in this case. Far more light than dark moths were captured by birds in the Birmingham area, while the reverse was true in Dorsetshire.

Although this study has many interesting implications which are beyond the scope of our discussion, let us attempt to explain it in terms of the evolutionary factors we have introduced in this chapter. Analysis reveals that the difference between light and dark forms of this moth is controlled by genes, which means that mutation and recombination accounted for the original appearance of dark forms. Even under intense selection pressure, these genes would not disappear from the population because of the continued recurrence of mutation and recombination. With a change in the environment, however, natural selection (differential reproduction) enabled the dark forms to gradually outnumber the light ones. Given some form of reproductive isolation, each variety might eventually form a distinct race, subspecies, or species.

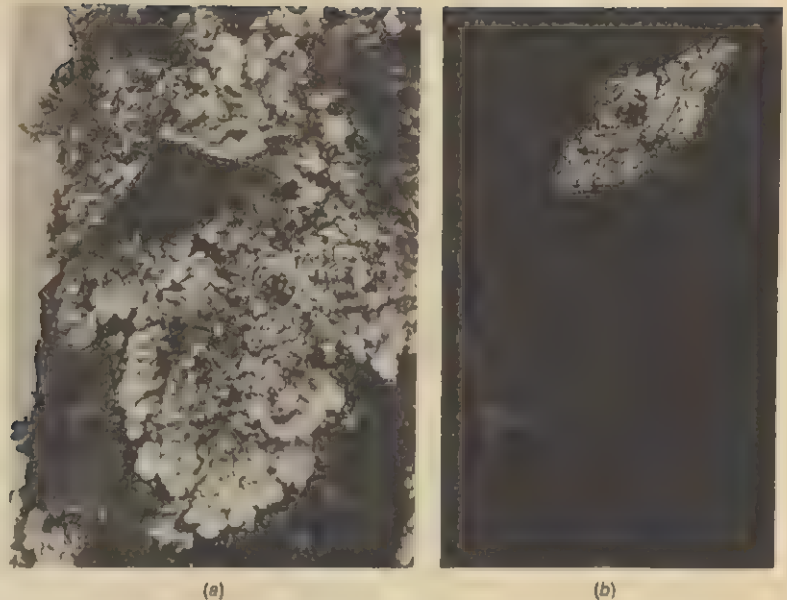


Figure 11.6 Light and dark forms of the peppered moth in contrast on (a) lichens and (b) a sooty tree trunk. It is not difficult to visualize how natural selection occurs in each case. (From the experimental work of Dr. H. B. D. Kettlewell.)

At this point, let us return briefly to a consideration of the four major factors of evolution which we introduced and discussed earlier. To a person acquainted with Mendelian genetics, recombination is not difficult to understand in its application to evolution. To a student of nature, there should be no question about natural selection and reproductive isolation. That the process of mutation should account for the origin of variations, however, and thus provide the raw material for evolution, is difficult for some people to accept. Probably, this is because they are aware that most mutations are "bad," and since any organism in which a mutation occurs is a member of a species that is already adapted to its environment, it appears unlikely that a mutation could improve its fitness.

There are at least two points which should be emphasized in consideration of this problem. First of all, assuming constancy of environment in any particular case, no species is so perfectly adapted that it cannot be improved. Mutations are not necessarily harmful; we tend to think of the bizarre examples often used in elementary genetics, such as certain types of idiocy in humans or winglessness in fruit flies, which are traits that depend upon single recessive genes in a homozygous condition. For the most part, mutations apparently influence traits in a quantitative way, and it takes special techniques to detect them. Many of these genes are potentially beneficial to the species, and we have seen how the condition of diploidy makes it possible for such genes to remain hidden until

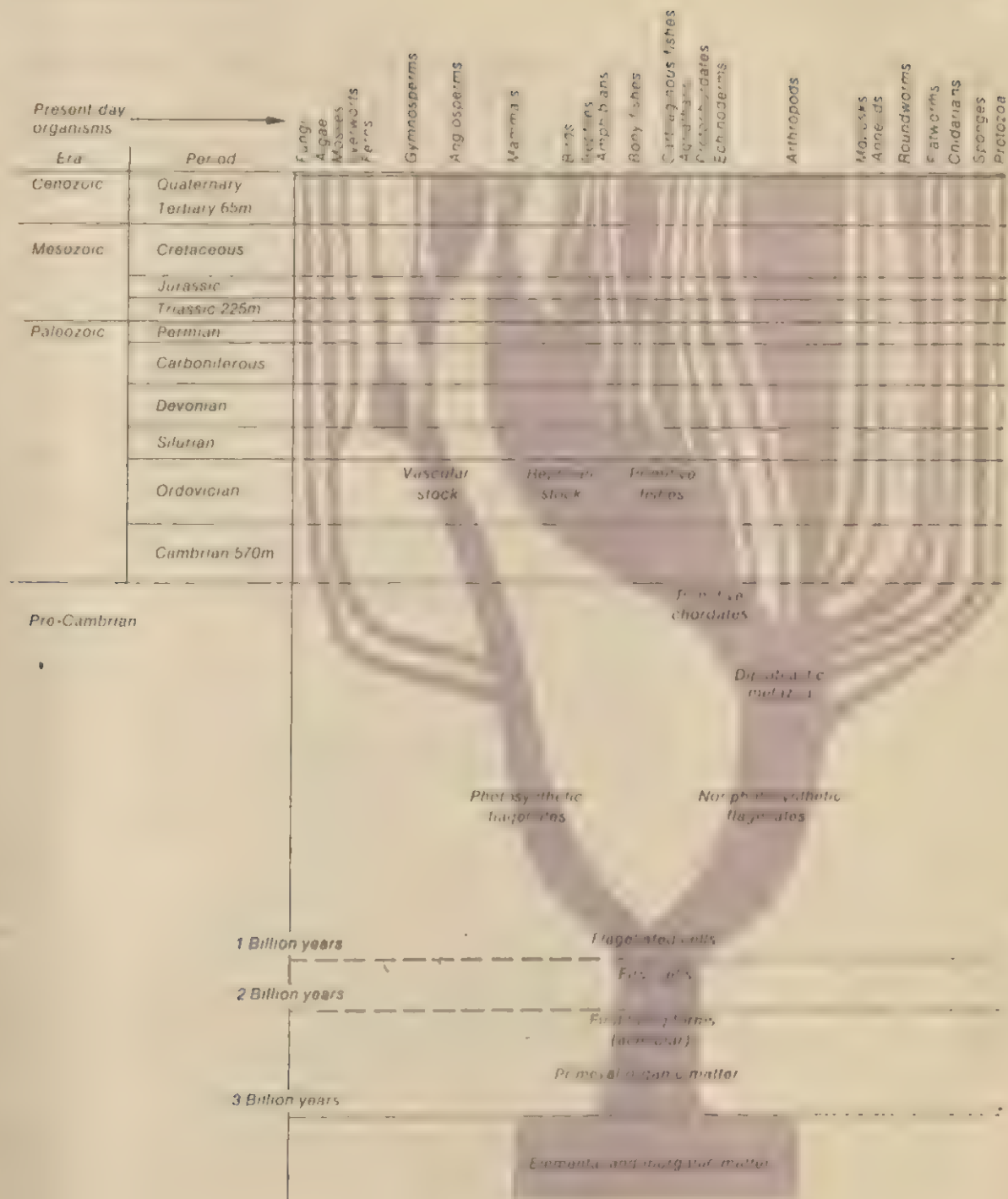
such a time as they might spread by natural selection throughout a population. Secondly, the environment might change so that a previously harmful gene becomes beneficial. We saw an example of this in Kettlewell's work, reviewed above. Let us consider still another case. Wingless fruit flies are at a decided disadvantage to those with wings in most environments. Several years ago (and this experiment has been performed more than once) a mixed population of winged and wingless flies was taken to a windswept island region where virtually all insects were wingless. Presumably, the environment here favored wingless insects, and natural selection weighed heavily against winged forms. Upon releasing a mixed population and making periodic collections, it was found that only wingless forms endured for very long. In a control group, under conditions where wind was not an environmental factor, the very opposite was the case. Hence, winglessness in flies is neither advantageous nor deleterious, *per se*; it all depends on the environment. Within recent years, experiments with bacteria (which reproduce so rapidly that results can be obtained in a very short time) reveal that a number of "bad" mutations in one chemically defined environment are "good" in another. Hence, we see that mutation, recombination, and natural selection all work together in determining fitness.

Perhaps it is apparent by this time that the process of adaptation occurs through the forces of evolution. Lamarck correctly emphasized the importance of adaptation to the world of life, but failed to identify the mechanisms by which it comes about. Darwin correctly emphasized natural selection as a mechanism of evolution, but failed to explain other factors. It remained for others to supply the missing pieces to the puzzle, and today, the synthetic theory apparently takes into account the major factors of evolution.

11.5 On the basis of available evidence from paleontology, evolution has proceeded very much according to the pathways diagrammed in Figure 11.7. Unfortunately, the fossil record does not extend as far back as a billion years, and even in rocks that can be identified as being almost this old, recognizable fossils are rather scarce. Organic materials found in older rocks, however, indicate that life originated considerably more than a billion years ago. Beginning with rocks that are almost a billion years old, enough fossils have been un-

**The course
of evolution**

Figure 11.7 The course of evolution, indicating the approximate time when a group of modern organisms arose and something of the relative numbers of extant species. Because fossils from the Pre-Cambrian are rare, that portion of this diagram is built largely upon inference.



covered to enable paleontologists to establish a general pattern. Figure 11.7 indicates probable origins and relationships of only major plant and animal groups; for further details regarding any particular group, the student is urged to consult a textbook of paleontology or evolution.

It should be pointed out that many animal and plant groups have arisen and have later become extinct. No attempt is made in Figure 11.7 to indicate these groups, but many are well known to paleontologists. One of the best-known examples of extinction is the case of the dinosaurs, a group of giant reptiles that flourished during the Mesozoic era. Apparently, they were unable to meet the general environmental and biotic changes which occurred during this time, and they ultimately perished. Undoubtedly, this pattern of the rise and fall of species (and more inclusive taxonomic categories) has played an important role in the process of evolution.

The pattern of evolution, then, should be visualized as a branching tree whose separations into more and more diverse groups have continued over tremendous periods of time to the present day. According to this concept, no present-day species necessarily ascended (or descended) from any other present-day species, but groups of organisms that are closely related structurally and functionally share a common ancestry.

Attention has repeatedly been called to the principle that certain biological mechanisms are shared either by all organisms or by large groups. For example, the ATP-ADP energy system, mitosis, meiosis, and photosynthesis were apparently such successful adaptations that they became firmly established as a way of life. In the light of the evolutionary concept, it is most significant that organisms share many fundamental processes in common. Since in the final analysis all living processes are controlled by genes, this indicates that some must be shared (perhaps in identical DNA structure) by all living forms.

It has been pointed out that metabolism, growth, reproduction, and responsiveness are characteristics of protoplasmic systems as such. Adaptation, in contrast, is not a characteristic that can be readily demonstrated in the laboratory, although such work as that of Muntzing on *Galeopsis* (called *species synthesis*) does constitute a demonstration of evolution. One must visualize the process of adaptation as an inherently long-range characteristic the results (though not many of the specific operations) of which can be seen. Thus, the evidence indicates that organisms have adapted through evolution, but we did not see them adapt. Nevertheless, it is possible to trace the adaptations of populations through careful statistical studies, and we are not entirely in the dark as to the workings of the process. Of much more value to us in this respect, of course, are the evidences

of evolution (such as the fossil record) which were presented earlier in this chapter.

Let us make one final observation with regard to adaptation. In the overall analysis, the characteristics of metabolism, growth, reproduction, and responsiveness are adaptive. For example, we have chosen in this book to discuss heredity within the framework of reproduction. Actually, it is an important part of adaptation, since the segregation of genes in meiosis and their recombination in fertilization determine to a great extent the role that an individual will play in its environment. Again, the same might be said for mechanisms of responsiveness, growth, or metabolism. It is the whole organism and the species to which it belongs that must survive and reproduce in its environment, and it is only within limits set for teaching purposes that we are justified in viewing the world of life from the standpoint of five characteristics. Books, not organisms, are separated into chapters. The phenomenon called life is dependent for its maintenance and perpetuation upon the coordination of all protoplasmic and organismic mechanisms, and it is only through this concept that we can view the world of life meaningfully.

Having given some attention to each of the five characteristics of living forms and realizing that these characteristics are highly coordinated in the organism, we bring to a close the purely informational aspect of our subject. How does this body of knowledge (which has been presented only in survey within this brief text) relate to all knowledge, and what is its significance to man as a species? We shall seek some of the answers to these questions in the next (and final) chapter.

11.6 The world of life as we know it today is the result of a long process of evolution. A great many present-day species have endured for long periods of time without appreciable change, whereas others are relatively new. Adaptations of various organisms have apparently arisen by the complex interaction of the forces of evolution. These forces are mutation, genetic recombination, natural selection, and reproductive isolation. According to the modern synthetic theory, evolution and adaptation are to be accounted for by these four factors.

Questions

1 Advance some possible reasons for the fossil record's incompleteness.

2 What is a comparative serological test? Of what value is it to the evolutionist? To the taxonomist?

3 Since the majority of mutations are harmful to the organism in their expression, how can mutation as a process be considered the primary source of genetic variation in evolution?

4 Wallace and Srb (see reference below) define evolution as "a change in the hereditary characteristics of successive generations of a population." Clearly, this defines evolution as a process. Would this also serve as a definition of adaptation? These authors continue with the observation that, according to this definition, adaptation is evolution, but that evolutionary changes are not necessarily adaptive. Can you explain this relationship between adaptation and evolution?

5 When the science of genetics began to develop early in the present century, it appeared that it would completely invalidate Darwin's theory of natural selection. What was the apparent conflict, and how has it been resolved?

6 We defined natural selection as being essentially differential reproduction. What is meant by this expression? How does it relate to Darwin's phrase "the survival of the fittest"?

7 What role do you suppose chance plays in evolution? How might it have an important influence upon each of the four factors of evolution discussed in this chapter?

8 Read and evaluate the third chapter in Ross (see reference below) entitled "Life: Its Nature and Origin." This is an excellent summary of the research which pertains to this subject.

9 For a concise summary of the history of evolutionary thought in biology, read Simpson's (see reference below) Chapter 16, "Historical Retrospect: The Evolution of Evolution." Do you feel that Simpson and other evolutionists are too mechanistic in their explanations of evolution? Relate Simpson's last three paragraphs in this chapter to our earlier statement (Chapter 1) that "the scientist, as a scientist, must act as if [questions pertaining to metaphysics and first causes] have no meaning for him."

10 Perhaps Question 9 at the end of Chapter 2 will have more meaning for you now than it did at that point in your course. Read it again and develop an answer based on the knowledge and insights you have gained since you first considered it.

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Biology, evolution, and human affairs

At one time in the history of civilization, a learned man made little attempt to become an intellectual specialist; he merely served his society as a *philosopher* and was interested in all knowledge. Although the modern philosopher still serves in something of the same capacity—attempting to coordinate the several intellectual areas into a meaningful whole—most present-day scholars feel obliged to concentrate on one particular field such as biology, sociology, or mathematics.

In one sense, this specialization is unfortunate because it deprives the specialist of a broad view which might help him to communicate more easily with other specialists. Furthermore, his own field frequently suffers from sheer isolation. Since human knowledge is now so vast, such a system of specialization is inevitable, but no intellectual person should cut himself off from fields other than his own. Furthermore it is particularly important that the student seeking a liberal education attempt to interrelate his studies. Regardless of how much he may specialize later, his undergraduate education should be directed toward an understanding of the world as a whole and not toward isolated aspects of it.

This final chapter, then, represents an effort to relate the subject matter that has been presented thus far to at least some other areas of learning. At the same time, it will be worthwhile to examine certain philosophical implications of biology.

12.1 Biology and evolution

Biology has always been an important science from a practical standpoint, serving as it does such applied fields as agriculture and medicine. Furthermore, man himself is an organism, and the theories that he formulates with regard to other organisms usually have an important bearing on his own welfare. Psychology and medical research have utilized this principle very effectively through the experimental approach based on the reactions of laboratory animals to conditions set by the researcher.

Although these practical contributions of biology to the welfare of mankind are highly important, it is in an altogether different realm that biology has made its greatest impact upon society—the realm of ideas. An idea or great conceptual scheme in any field that can fire the imagination and proves to be productive of other ideas or technological developments is always of far-reaching importance, and all too seldom are such conceptual schemes formulated. Thus far in biology, there has been one outstanding idea (among less engaging but perhaps equally important ideas) that has had a profound influence upon human thought, and this is the concept of evolution. It is to this subject that we shall now turn our attention.

Evolution and man It was mentioned in the preceding chapter that Darwin initiated something of an intellectual revolution in 1859

by publishing *The Origin of Species*. Historians are aware that a number of factors were responsible for the general public reaction to this book, and many of these could be discussed at this point very profitably. However, two reasons for this reaction seem outstanding. First of all, the concept of evolution, which was not widely accepted by lay persons at that time, stood out in direct opposition to the literal interpretation of the Genesis account of creation which was widely accepted in those countries that were predominantly Christian in their religion. We shall defer a discussion of this factor until later. The second factor, and one that was more fully emphasized in a later book by Darwin, *The Descent of Man*, was that the concept of evolution applied, by implication and by direct evidence, to man himself; and this concept identified his biological nature with that of other higher animals.

It is quite understandable that, in mid-nineteenth-century England, this latter idea would provoke a widespread revolt. Even today, one frequently encounters a person who refuses to accept the animal nature of man. Yet, it is inevitable that, once having accepted the general principle of evolution, one is obliged to extend it to man also. It is not within the scope of this brief text to review the considerable evidence of man's evolution, but it should be mentioned that all the lines of evidence discussed in the preceding chapter point to man's close genetic kinship to (but not necessarily descent from) other existing primates. Although this was a disturbing thought to most people of Darwin's time, and it is a topic that can still arouse heated discussion in many circles, the evolution of man is generally accepted.

Evolution and religion In view of the fact that any religion must ultimately evaluate man, his dignity, and his place in nature, it is not difficult to understand why evolution became a matter of concern to religion as soon as Darwin made it a matter of concern to science. It immediately became necessary for religion to debate within its own ranks whether the link which evolution declared to exist between man and other organisms was degrading, uplifting, or neither. At first, opinion among religious leaders generally was that evolution deprived man of his uniqueness and reduced him to a mere animal. Around this point centered some of the most heated debates ever witnessed by the intellectual world. In fact, during the latter portion of the nineteenth century, the rift between biology and religion became so great that in most civilized countries an attitude of "science or religion, God or evolution" prevailed. This rift has not entirely healed in the minds of a great many people, and to them, even the word "science" may be associated with complete rejection of religion.

Although many leaders of religious thought during this time were characterized by the position stated above, some adopted the view that it was not degrading at all, but actually uplifting, to realize that man held actual genetic kinship with other organisms. According to this interpretation, man should feel that his emergence as a uniquely gifted species from the biological shackles of past ages was a matter of pride rather than shame. In an attempt to reconcile evolution and religion, many proponents of this view adopted the philosophy of *theistic evolution*; that is, they saw evolution as a divinely guided process. The point with them was no longer "God or evolution," but "God through evolution."

Perhaps the more thoughtful of the nineteenth-century theologians were never greatly concerned with the evolutionary implications of man's animal nature. However, they were disturbed by Darwin's expression "natural selection," which implied that the universe runs on chance events. This, in turn, appeared to negate the direct operation of God in nature. Earlier in the nineteenth century, theology had been challenged by the philosophy of *positivism*, and with the publication of *The Origin of Species*, it was obliged to deal seriously for the first time with the question of *teleology*. Let us digress at this point to consider these terms and the ideas they represent.

The philosophy of positivism arose in Europe during the early part of the nineteenth century partly as a reaction against dogmatic theology and partly as an accompaniment to the brilliant successes achieved in the natural sciences just prior to and during that time. Developed and cultivated chiefly by the French philosopher Auguste Comte (1798–1857), it stressed "real and useful" knowledge as contrasted with theological and metaphysical avenues of thought. In fact, positivism would explain everything in terms of natural causes, and this, of course, aroused the opposition of the clergy. Furthermore, Comte had written at length on biology and evolution (although his ideas were quite deficient by modern standards), and he had done more than any other nineteenth-century thinker, perhaps, to pave the way for an acceptance of Darwinian evolution. As a consequence, natural selection suffered a degree of guilt by association, although it implied enough on its own to alarm most theologians of the period.

Teleology is the philosophy or viewpoint that development, whether in an organism or in evolution, is purposeful and goal-seeking. It is also called *finalism*. To illustrate, if we say "the purpose of the higher animal brain is to coordinate nervous impulses," we imply design and externally imposed goals for the species in question. Present-day scientists reject teleological explanations because they

are not subject to experimental analysis. You will recall that our first assumption in Chapter 1 (Section 1.1) was concerned with this limitation of science. During the nineteenth century, both science and theology were saturated with teleological viewpoints. Few in science had defined their methods and limitations rigorously, and natural theology (seeing God in nature through design) was the fashion in religion. As a result, it had become a habit with virtually everyone to view adaptations—especially those characterizing the human—as evidences of divine design. Within this framework of thought, it is small wonder that Darwin's frontal attack on teleology (remember, he called it *natural* selection) was offensive to most theologians of the period.

It was mentioned earlier that an important cause of conflict between evolution and religion centered around the *Genesis* account of creation.* This conflict reached its peak early in the twentieth century, when the fundamentalist movement in religion became widespread. According to the traditional and literal interpretation of *Genesis*, God first created the inanimate earth and then proceeded to create living forms successively; preparation of the earth for these forms and their creation occupied a period of six days. Also traditional with this viewpoint, although not stated in the actual account, was the interpretation that living forms were immutable (not subject to genetic changes that would cause the production of other species from them).

Obviously, a literal interpretation of the *Genesis* account is at direct odds with evolution. For those persons who accept the Bible as an inspired or God-given volume of writings, and yet who do not choose to blind themselves to the evidences, data, and methods of science, this poses something of a problem. Although the extremes of evolution and creationism appear to many people to be completely irreconcilable, others have found a satisfactory middle ground. If one accepts the *Genesis* account as a rather figurative and completely nonscientific narrative, according to this position, it becomes meaningful and highly accurate. Thus the figurative interpretation of *Genesis* is made to complement, not contradict, evolution.

This viewpoint, although not acceptable to fundamentalists, is widely held among present-day Jewish and Christian theologians and scientists. The following is from a representative and well-stated discussion of this aspect of science and theology by the biologist Edward McCrady. After comparing the sequence of events in *Genesis* with some of the high points of evolution, he continues:

*See *Genesis* 1.

On the whole, this is an excellent account—far and away the best of all ancient ones, and in some details remarkably modern. Probably no one would ever have thought of it as conflicting with science if it weren't for the word "Yom," meaning day, which fundamentalists take to mean a period of twenty-four hours. The great theologians of the fifth to the fifteenth centuries believed that it meant an era, or epoch, or indefinite period of time, as it does in English when we speak of what happened in Julius Caesar's day, etc. That the author of Genesis so meant it seems fairly obvious from internal evidence, for after describing in detail what occurred on each of six days, the author refers to the one day in which it all happened—"These are the generations of the heavens and the earth when they were created, in the day that the Lord God made the earth and the heavens" (Gen. 2:4).

If there is a difficulty for the modern reader in connection with the biblical account of creation, it is not the problem of reconciling it with science, but that of accounting for its remarkable adequacy. But it seems to me that there are much more important connections between the theory of evolution and Christianity than questions concerning the degree of scientific accuracy in Genesis. I am confident that the Bible was not intended to be a textbook of science, and whoever reads it for that purpose wastes his time, or, at any rate, misses his opportunity."

Today, the controversy between evolution and religion has largely subsided for the simple reason that, as philosopher John Dewey says, people do not really solve the great problems; they get over them. By one way or another, two viewpoints which appeared at one time to be irreconcilable no longer seem so far apart to serious students of both science and religion. For this reason, many excellent scientists (and many thorough-going evolutionists) have not found it inconsistent with the methods of science to accept metaphysical ideas or religious values. Those who have probed into the matter have either found an answer or else, as Dewey says, the question no longer seems so important. At the very least, one may be led to believe in a God who was responsible for the initial creation of matter, of energy, or of physical and chemical law. The possibility for such belief is stated by a present-day biologist as follows.

A theory of evolution that postulates that life arose by natural processes from nonliving precursors and achieved its present diversity, including man, through the natural selection of rare favorable rearrangements in the genetic material is on first thought abhorrent to many. It is a mechanistic view and it appears to conflict with the teachings of many religions. How, then, can it be accepted by science?

* Edward McCrady. *Biology*, in *Religious Perspectives in College Teaching*, by Hoxie N. Fairchild, et al. (New York: The Ronald Press Company, 1952).

It is true that the thesis here defended does conflict with the Bible as literally interpreted. In fact, any acceptance of organic evolution leads logically to such a conflict. One must accept all of evolution or none. And the evidence for organic evolution is overwhelmingly convincing.

The direct conflict is avoided by many through the acceptance of a nonliteral interpretation of religious gospel. Once this possibility is accepted, it can be argued that belief in evolution, including the spontaneous origin of life from nonliving antecedents, need in no way conflict with religion.

The argument can be put in the following way: Suppose one believes in a higher intelligence responsible for the creation and direction of the universe—a belief that is a matter of faith, for present science can neither prove nor disprove it. It is clear that such a supreme being did not create present man, for we have direct evidence of our immediate ancestors. One can then argue that what was created was rather ancestors capable of giving rise to us. How remote were they? Were they primitive men of a million years ago? Or were they perhaps preman ancestors? Once embarking on this line of thought there is no logical place to stop. One is led easily but firmly to the conclusion that the creation of a universe of elementary physical particles endowed with properties that made inevitable the evolution of elements and molecules and life when the conditions were proper is just as remarkable and just as deserving of awe and reverence as is the direct creation of man.

*Like the universe and like life, religions are not immutable. The ancestral forms of many of them conflict with modern science as do some of those that now exist. But the conflict is not necessary. And if man is to achieve the loftiest goals made possible by his biological and cultural evolutionary potentials, he must see to it that in the future religions and science evolve together in harmony.**

Evolution and society It seems evident that Darwin, who was certainly not a social revolutionist, never intended that his theory should extend beyond the scientific realm. The society into which he cast the concept of evolution by natural selection was, however, of such a nature that it was inevitable that all areas of thought should become affected by it. We have seen how this was true in religion. Not long after the initial clash between evolution and religion, it became intellectually popular to interpret every field in the light of natural selection. A number of books appeared in the latter part of the nineteenth century on the subjects of sociology, psychology, ethics, and political science with natural selection as their main theme. Indeed, it was a rare field of endeavor that escaped an evolutionary interpretation during this period. As one biological historian

* G. W. Beadle, *The Physical and Chemical Basis of Inheritance* (Eugene, Ore.: The University of Oregon Press, 1957). By permission of the Oregon State Board of Higher Education.

expresses it, "The generation to which *The Origin of Species* was delivered followed Darwin blindly."^{*}

A concept as intimately concerned with human life as that proposed by Darwin could not fail to exert very profound influences, not all of which were good, upon practical affairs. To men on both sides of the question, the logical consequences of the theory seemed to undermine the authority of moral values. It became evident in the decades following Darwin that this was not without its effects. That phase of natural selection which Darwin chose to term "struggle for existence" was particularly emphasized. It appealed very strongly to the apologists for war who saw a way for the strong to justify by "natural law" the conquest of the weak. In Germany, where a strong feeling of racial supremacy had already been carefully nurtured, the Darwinian concept of struggle for existence and survival of the fittest was received with particularly strong enthusiasm. During the latter part of the nineteenth century, her political philosophy became saturated with the doctrine of the right of the strong nation to deprive the weak of human rights. By 1914, this feeling had reached these proportions:

Wherever we look in Nature we find that war is a fundamental law of development. This great verity, which has been recognized in past ages, has been convincingly demonstrated in modern times by Charles Darwin. . . . The struggle for existence is ruled by biological laws.[†]

Unfortunately, it was to take more than one great war to eradicate transplanted and misinterpreted Darwinism from the minds of political theorists:

We are all aware that in the future mankind will have to deal with problems, to cope with which some most noble race will have to be summoned as the master nation, supported by the forces of the whole globe.[‡]

Not only in terms of actual war, but in economic affairs, the 'struggle and survival' concept became popular. Karl Marx, the German economist who was contemporary with Darwin, found it easy to think of Darwin's species as being analogous to the "struggling" classes of economic society. Hence, it was only a step to the justification of ruthless business and economic practices which were based, as in the case of the waging of war, on 'natural law.'

In short, Darwin's theory of evolution was lifted from the field of

^{*} Charles Singer, *A History of Biology* (New York: Abelard Schuman Limited, 1959).

[†] Friedrich Bernhardi, *Britain As Germany's Vassal* (translated) (New York: George H. Doran Co., 1914).

[‡] Adolph Hitler, *Mein Kampf* (translated by Ralph Manheim) (Boston: Houghton-Mifflin Company, 1943).

biology during the nineteenth century and was applied to virtually every area of human thought. It certainly was not Darwin's intention that this should happen because his expressions were metaphorical in nature, and he dealt to a great extent with analogies. However, he was made to say a great deal more than he actually said.

*Darwin had tried, once or twice, to show his metaphors for what they were, but few read him. They read his expounders instead who dramatized the "story of evolution" by stressing the business of chase, capture and death. It was always a tiger and a gazelle, and a gazelle with slightly longer legs. To accept the absolute value of survival, the common mind wanted it to represent a 'genuine' value. It would have been horrified to learn that 'fittest' only means 'those who survive,' and that the sickly coddled child of wealth who lives and procreates is fitter than the robust laborer who dies of overwork and bad food.**

Even in biology, we have had to revise our thinking about natural selection. Let us be careful to remember that Darwin conceived of it in somewhat narrower terms than we do today. In other words, the concepts of "struggle for existence" and "survival of the fittest" not only are unjustifiable in social relations, they have unfortunate connotations even in biology. Darwin himself used these expressions only in a metaphorical sense; today, we use the term "competition" to replace the phrase "struggle for existence," and the fittest, as Barzun says, are simply those that survive. It seems never to have occurred to most people of Darwin's time that plants may struggle (compete) for light or moisture; they labored under a literal misunderstanding of his expressions. In fact, a second look at natural selection in terms of the animal kingdom alone revealed to biologists of a later generation that the concepts of "struggle" and "survival" had been greatly overemphasized:

It is a misfortune to suppose that Natural Selection implies a keen struggle and survival through brute force, for in many species cooperation, altruism of certain sorts and self-sacrifice are elements of the utmost importance in racial success.†

The fact is that the struggle for existence need not be competitive at all. • The world is not only the abode of the strong; it is also the home of the loving.‡

The historical lesson of society's experience with natural selection should not be lost on modern man. It is dangerous to draw

*Jacques Barzun, *Darwin, Marx and Wagner: Critique of a Heritage* (Boston: Little Brown and Company, 1941). Reprinted by permission.

†H. H. Newman, *The Gift of Evolution* (New York: The Macmillan Company, 1926).

‡J. B. S. Haldane, *The Causes of Evolution* (New York: Longmans, Green & Co., Inc., 1932).

analogies too freely between fields, especially when the basic premise is only a first statement in the field from which it is transplanted. Darwin's theory of evolution, which lacked completeness, was inadequate even in biology. How much more inappropriate it proved to be as a social theory is now obvious.

Evolution and biological philosophy Today, we take for granted the materials and methods of science and the validity of cause-and-effect reasoning. For centuries before Darwin's time, however, this was not the case. Biologists were divided over two philosophies of living processes, which we now call *mechanism* and *vitalism*.

Mechanism is a view of nature according to which matter and energy are involved in every phenomenon that occurs in the universe. As applied to organisms, it views life processes as being completely explicable by the principles of chemistry and physics. In some form or other mechanism is a very old explanation, and it has frequently arisen as a reaction against magic and superstition. It thrives upon scientific progress; in fact, the basic assumptions of science (Section 1.1) are essentially mechanistic, at least by implication. To a mechanist, then, the organism is essentially a complex unit of matter in which energy changes are taking place.

Vitalism, which is also a very old explanation of the nature of life, has taken a number of forms. As a modern scientific and philosophical view, however, it was developed chiefly by the embryologist Hans Driesch (1867-1941). Essentially, it holds that life processes depend upon forces that exist in addition to physical and chemical ones. It has developed most whenever extreme mechanistic views became prevalent. In a sense, therefore, mechanism and vitalism are reactions to each other.

It is not within the scope of this book to attempt a determination of whether mechanism or vitalism is the "truth." Each has its weaknesses, and each is quite possibly an extreme view.* However, mechanism is a far more fruitful viewpoint in biology, simply because vitalism is a poor base of operations for doing scientific work. In other words, the biologist is obliged to act as if mechanism is true. Only if the organism is approached as a bundle of matter and energy does the biologist ever come to explain its operations in scientific terms.

To return to Darwin and nineteenth-century Europe, mechanism was much more widely accepted in the physical sciences than in biology. No doubt, the vast majority of biologists were vitalists. A

* A number of alternatives have been proposed to these two extremes, the most generally satisfactory of which is *organicism* or *holism*. Almost any introductory textbook of philosophy includes a discussion of mechanism, vitalism, and organicism, and you may wish to pursue the matter further through such reading.

great many of them believed in spontaneous generation and (quite literally) in the magical operation of living processes. Inevitably, though, a reaction against this attitude came about. Descriptive biology, which barely qualified as a science at the time, managed fairly well with vitalism as an underlying philosophy. But the time was ripe for biology to enter a new phase of experimental activity and to mature into scientific respectability. It was within this framework of incipient emergence that Darwinism was born.

Actually, this seems to have been the cause of the great appeal of *The Origin of Species* to biologists. In many respects it was not a great scientific work, and it has been subjected to considerable criticism on purely scientific grounds. That Darwin's insights were clear and prophetic cannot be denied, but his arguments were rather vague. William Irvine (see reference at end of chapter) observes that Darwin had not so much proved that natural selection *does* occur as that it *must* occur. His point is well taken.

Darwin happened to come up with what historian Barzun calls the "right wrong" answer to the vitalism-mechanism controversy. Evolution was not so much accepted by nineteenth-century biologists because Darwin proved it, but because he pointed the way out of vitalism. Once it was accepted that the variety of living forms could be accounted for by natural processes, the door was open for the extension of mechanism to other phenomena of living systems. Without doubt, the concept of evolution as opposed to special creation solved the greatest of all possible problems for the mechanist. Once having embraced mechanism for the origin of species, it was easy to accept it for other life processes, as a *working principle*.

A great many people, including some biologists, view the philosophy of mechanism with suspicion because it would seem to imply a denial of God. Actually, as was stated for the concept of evolution in the preceding chapter, such a conflict is not necessary. Mechanism does imply, however, that any supernatural force must operate within natural processes. Accordingly, there are many biologists and other scientists who are thoroughly mechanistic in their approach to research but who maintain a belief in a highly personal God. This apparent paradox is tentatively resolved by the assumption that mechanism and vitalism are not *either-or*, but *both-and* issues. In its most refined form, this reconciliation of issues is known as *theological dualism*.

The concept of evolution has altered biological philosophy in still other ways and has opened pathways to knowledge that could never have been attained otherwise. To say the least, it has stimulated a tremendous amount of thought and has caused man to reexamine such issues as determination and free will, matter and spirit, and to

seek seriously a philosophy of life that is at the same time satisfying and consistent with the methods of science.

12.2 Of necessity, we have been concerned entirely in this book with the
The future past and present of biology. What of the future? One of the rewards
of biology of living in a civilization whose events move rapidly is the excitement that comes from anticipating major changes within fields of knowledge. If the past is any indication, we may expect a great many developments in biology within a few years. Some of the most interesting possibilities are discussed below.

The theoretical and the practical As we have observed, the biologist is somewhat dissatisfied with his present definition of life. In many respects, he is almost obliged to regard this phenomenon vitalistically, and yet he knows that only a mechanistic approach to the problem will yield further knowledge. We may expect to learn a great deal more about the nature of life within the next few years, and with such theoretical knowledge will come the understanding and conquest of such abnormal manifestations of life processes as cancer and feeble-mindedness in man. These are exciting challenges to the biologist, and it is conceivable that within a relatively brief period of time we shall discover a principle or principles of life as profound in their influence as evolution was to nineteenth-century biology or as the Einstein equation has been to twentieth-century physics.

Another exciting prospect which may be within our grasp is the possibility of discovering life elsewhere in the universe. From what we know of our own planet and of the conditions that apparently gave rise to life upon it, there is no reason why life may not also have originated on one of the thousands of planets whose environmental conditions may parallel those of our own. What will we find to be the forms of such organisms? Once we have first-hand evidence of the existence of other life than that we know, we shall open a new chapter in the history of biology.

In the meantime, there are more practical problems to be dealt with. Given a better understanding of marine ecology, we shall solve many of the world's food problems. Our greatly improved agricultural methods have already gone far toward this goal. One day, we shall learn to mimic nature in the large-scale production of carbohydrates through the combination of carbon dioxide with water, and this will contribute greatly to the solution of the problem. There are unconquered diseases that will be completely brought under control through continued research, and many of the knotty problems of psychology and philosophy that await biological explanations will be

made clearer. These are but a few of the practical triumphs of biology that most of us can expect to see within our lifetimes.

The future of man Man has apparently not undergone significant physical changes within at least 40,000 years. This does not mean that man is removed from evolutionary forces (although he constitutes something of a special case) but it does indicate that he has achieved a certain degree of physical stability. This is not at all unusual in evolution; modern cockroaches, king crabs, and opossums are virtually indistinguishable from their ancestors who lived millions of years ago. Most students of human evolution feel that man has reached a high degree of physical stability, and that the forces of evolution are not likely to modify him drastically, at least within the near future.

In view of the several considerations involved, it is highly improbable the human species will give rise to the supermen of science fiction. On the other hand, there is a distinct possibility that man can create conditions that will definitely degrade him. The outstanding danger at the present time consists of radiation hazards. With an increase of ionizing radiations in his environment, man is running more and more risk of acquiring serious genetic damage. As we have observed, ionizing radiations increase natural mutation rates in proportion to the strength of dosage, and such mutations are entirely random. Since most mutations are harmful ones, and because the majority are recessive, a single nuclear war could do far more damage to the human species in the long run than merely killing a few thousand or million people. For generations following such a holocaust, the induced mutations in sensitive germinal tissue would keep cropping out. Unless we take strict measures to control the disposal of certain radioactive wastes from industry, and unless we take greater precautions in regard to the needless exposure of human beings to X rays, we may be in for serious trouble. This is not to suggest that nuclear reactors and X-ray machines do not have a definite place in our society; both have more than proved their usefulness in terms of human welfare. Nevertheless, exposure of human tissues, and especially germinal tissues, to radiation is a very serious matter and one that has caused many biologists to become thoroughly alarmed. Here again, we see that what might appear to be a political or social problem is actually a biological one, basically. A more indirect but perhaps equally serious danger to civilization as we know it lies in the population explosion that the world is now experiencing. Like other biological problems that we have discussed, this one is accompanied by economic, political, and ethical overtones. Furthermore, as is the case with all such interdisciplinary problems, we are going to have to make some difficult

decisions; in this case, they will have to be made with regard to birth control and a wiser use of the earth's available space. Because these problems must be dealt with in one way or another, the present-day citizen owes it to his society to become well informed about them.

However, returning to matters of man's evolution, there are those biologists who suggest that just as man's physical evolution may have come to a virtual end, he is on the threshold of new heights in an entirely different realm—the evolution of the spirit. Whether one conceives of the spirit of man as a matter of personality or as a divine investment, this is an intriguing possibility. All are agreed that mankind could be less "animal" and more "spiritual" in nature, but until relatively recent years, it had occurred to few biologists that they had any stake in the area; traditionally, it has been the concern of philosophy and religion, in the main.

Without doubt, there are principles to be found in biology that help some persons to arrive at a more satisfying philosophy of life than if they had not studied the subject. Certainly, a large number of books have been written on the subjects of spiritual evolution and human destiny, many of them authored by outstanding biologists. Probably most biologists feel, however, that these are matters that must ultimately become the concern of religion, not biology. Although religion and biology have much to offer each other, they still must travel two separate roads toward their respective truths. It is the task of biology to observe, to experiment, to learn more about natural phenomena, it is the task of religion to relate man to ultimate reality. Whether man has a divine or a purely human destiny is not a matter for biology, as a field, to decide. This is a far cry, of course, from saying that biology is opposed to religion. It is simply that the biologist, as such, is bound to the basic assumptions of science, and religion is not scientific. It deals, of necessity, with matters that are not subject to experimental analysis.

However, what of man's future in his world community? Here, he has a destiny to fulfill, and he must fulfill it if he is to survive. The next few decades must see moral and ethical values catch up with technological and scientific knowledge. Here again, religion and philosophy must take the lead, but on this point biology can be of help. Perhaps the one thing that all biologists have in common, no matter how diverse their special interests, is their concern for life. Unable to agree on an exact definition for the phenomenon, they nevertheless all esteem it highly enough to devote their energies to some aspect of it. The biologist is therefore in a unique position to appreciate the need for measures that will ensure world peace and that will prevent the needless loss of human life. That there is a direct connection between a desire for the preservation of life and

respect for it as a biological phenomenon is illustrated by the following statement from a contemporary cytologist:

*The more we delve into these problems, the more life remains mysterious. All that we can do is to contribute by our work to the solution of the biological riddles. But, what we must also do, is to admire, respect, and love life; we must protect it, and not destroy it. We, biologists, must work more than anybody else for peace among men.**

Most biologists, regardless of how much they might disagree on philosophy, religion, or even biology, are in wholehearted agreement with this sentiment.

Questions

- 1 Is the term "Darwinism" synonymous with the term "evolution"? Explain.
- 2 Explain the difference between vitalism and mechanism.
- 3 To what extent did nineteenth-century ideas of evolution apparently contribute to the causes of the world wars of recent generations?
- 4 Can one be a mechanist and still believe in God? What is your personal feeling in this matter?
- 5 Why was Darwin's theory of evolution so widely accepted in spite of its apparent weaknesses?
- 6 Do you think that life exists on other planets? Read the interesting and thought-provoking discussions of this subject by Eiseley (see reference below) and Simpson (*This View of Life*, reference at end of Chapter 1).
- 7 Do you believe that a living organism will ever be synthesized or created from nonliving material by man? Assuming that this is accomplished at some time, what influence (if any) will this have on the argument for or against the existence of God?
- 8 Why are ionizing radiations dangerous to man in the long run?
- 9 Evaluate Edward McCrady's attempt to reconcile evolution and the *Genesis* account of creation. Would an acceptance of this view of *Genesis* necessarily make one a theistic evolutionist?
- 10 Section 12.1 reviews some of the effects of "social Darwinism." You might be interested to learn how Darwin's hypothesis regarding genetic mechanisms has been distorted within recent decades to form a "scientific" basis for the party line of communism. Hardin (see reference below) presents a brilliant summary of this development, which culminates with his Chapter 11, "Liberalism and the Spectre of Competition."

*Jean Brachet, *Biochemical Cytology* (New York: Academic Press, Inc., 1957).

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In addition to these books, the following articles from *Scientific American* are recommended.

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Erseley, L. C. "Is Man Alone in Space?," Vol. 189, July, 1953. An interesting speculation on the subject of the article.

Puck, T. "Radiation and the Human Cell," Vol. 202, April, 1960. A good discussion of the mode of action of ionizing radiations and the extent to which human cells may be affected by them.

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